

A PALYNOLOGICAL STUDY OF TWO OF THE NEOGENE PLANT BEDS IN DERBYSHIRE

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CONTENTS

	<i>Page</i>
I. INTRODUCTION	362
II. CLASSIFICATION AND NOMENCLATURE	362
III. METHODS	366
IV. SYSTEMATIC PART	367
Sphagnaceae	369
Lycopodiaceae	370
Gleicheniaceae	371
Osmundaceae	371
Polypodiaceae	372
Schizaeaceae ? / Polypodiaceae ?	373
Taxodiaceae	374
Pinaceae	375
Podocarpaceae ?	379
Papilionaceae ?	380
Symplocaceae	381
Nyssaceae	381
Araliaceae	382
Hamamelidaceae	383
Salicaceae	384
Myricaceae	384
Betulaceae	385
Fagaceae	386
Corylaceae	387
Juglandaceae	387
Ulmaceae	388
Aquifoliaceae	388
Sapotaceae	389
Ericaceae	390
Onagraceae	390
Compositae	391
Liliaceae	391
Graminae	392
V. QUANTITATIVE ANALYSIS	392
VI. AGE DETERMINATION	399
VII. THE NEOGENE ENVIRONMENT IN DERBYSHIRE	402
VIII. ACKNOWLEDGMENTS	405
IX. REFERENCES	405

SYNOPSIS

Two of the sink hole deposits on the Derbyshire Carboniferous Limestone outcrop have been found to contain plant bearing clays. The pollen and spores that have been isolated from this

material are identified in terms of modern genera or form genera and species. Some of the 63 taxa which are described are shown, by comparison with fossil material from the continent of Europe, to be representative of Miocene and Pliocene deposits, and a Miocene/Pliocene boundary age is suggested for the assemblage. Quantitative pollen analysis from a vertical section through one of the deposits shows little variation in the floristic components, although there is a substantial change in the absolute concentration of palynomorphs. This suggests that the whole of the deposits, together with their contained pollen, may have been redeposited from a higher surface. Concordant with this concept is the separation within the assemblage of two floristic regions, one of heathland and the other of mixed woodland. The significance of the components of these floras is discussed in relation to plant distribution from the beginning of the Tertiary to the present day.

I. INTRODUCTION

A BRIEF description of some of the plant microfossils and macrofossils from two of the sink hole deposits (often called pocket deposits) in Derbyshire (Bee's Nest pit and Kenslow Top pit) have been given recently by Boulter & Chaloner (1970). While there is apparently no extempore geological method by which their age can be determined, palynological evidence does suggest a Neogene age, most probably Lower Pliocene. This age determination is of significance not only to the geomorphology of the whole deposits themselves, but also to Pennine uplift in general. What follows is an account of the pollen and spore assemblages found in these fossil plant bearing deposits. As it is the only study of Neogene palynology that has been made in the British Isles, its interpretation hinges largely on comparison with Continental assemblages of similar age.

There is a very large number of Neogene localities on the Continent of Europe which are of interest to the palynologist, though not all are of equal relevance to the Derbyshire assemblage. This is due not only to the regional variation of Neogene floras within Europe itself, producing what are often referred to as Facies Elements, but also to difficulties in correlation and palynological identification. Recently, some of the most crucial aspects of Neogene palynology, on a world-wide scale, have been concisely reviewed by Leopold (1970). Work from these centres has established the citation of palynological divisions within the Miocene and Pliocene; no single continuous Neogene sequence is known however, and correlation between the several sites is not well understood. Particularly important to the present study is the discontinuity at the Miocene/Pliocene boundary, which makes this one of the least understood parts of the Neogene succession in Europe. Also, a recent revision of the radiometric time scale in the Cenozoic, based on foraminiferal zones (Berggren, 1969) suggests a far more recent dating (about $5\frac{1}{2}$ million years) of this boundary within the marine succession itself than was previously envisaged. The palynological divisions within the Neogene of The Netherlands and West Germany, shown in Figure 1, are of most relevance to the Derbyshire assemblage, though the correlation of these to the marine succession, and their chronostratigraphic extent, are both uncertain.

II. CLASSIFICATION AND NOMENCLATURE

The nomenclature of Neogene palynomorphs presents a difficult problem, which cannot be satisfactorily resolved for all the disciplines concerned. The same rules of

nomenclature that are used by neobotanists can be followed in Pleistocene palynology since the identification down to a living species is usually possible, whilst in Palaeozoic and Mesozoic work botanical affinities can rarely be concluded with confidence so that fossil form genera and species are incorporated into one or other system of morphographic classification. But the Neogene palynologist finds that his identifications fall within both of these categories. Some specimens can be

		NETHERLANDS WEST GERMANY	
Pleistocene	lower	Tiglian Pretiglian	
	upper	Reuverian	Reuver Bild
Pliocene	middle	Branssumian	Fischbach Bild
	lower	Susterian	Posener Bild
Miocene	upper	Fischbach	Salzhausener Bild
	middle		Rheinisches Bild
	lower		

FIG. 1. Palynological divisions of the Neogene in The Netherlands and West Germany. The figure is not drawn to scale (see : Berggren, 1969), and the position of the Miocene / Pliocene boundary is only tentatively related to both series of divisions.

identified only as form genera and species, whilst others may be assigned to either modern genera or even to modern species. The resulting dissonance has been represented in many ways by different authors of Tertiary palynology (e.g. Thomson & Pflug, 1953 ; Traverse, 1955).

Normally, any Neogene palynomorphs that are encountered in European deposits can be assigned either to an extant genus or to a previously described form genus. And although some of the more recently created form species such as those of

Krutzsch (1962-1967) are delimited to a very narrow morphological range, earlier taxa such as those made by Potonié et al. (1950) and Thomson & Pflug (1953) are much more broadly circumscribed. So in the case of a commonly occurring Neogene palynomorph which cannot easily fit into a well defined form species or modern genus, use of the earlier more broadly defined form species can usually be made. All the palynomorphs that have been observed (in sufficient quantity—more than ten specimens) in the Derbyshire material, for instance, can either be attributed to a modern genus or else to a form genus with an established specific epithet. This practice must be interpreted most cautiously however, especially with regard to stratigraphic detail. Many of the taxa created by Thomson & Pflug, being of very broad circumscription, certainly represent more than one botanical species or even genus. Many have limited stratigraphic range and so are used as stratigraphic markers (Thomson & Pflug, 1953 ; von der Brelie, 1967). But since they are broadly circumscribed their known range is regularly extended as palynological work progresses, occasionally by forms slightly different from the type specimen but which none the less conform to the author's diagnosis. For example, in the Derbyshire assemblage, one pollen type is well described by a revised diagnosis for *Tricolpopollenites microhenrici* given by Thomson & Pflug (1953) ; some of their figures of this species are in agreement with the Derbyshire specimens too. But examination of their species from macerations of German browncoal show it to differ from the Derbyshire specimens in features not mentioned in the diagnosis (see page 386). Traditionally, this is sufficient reason for the creation of a new species, especially since *T. microhenrici* has been commonly regarded as a characteristic component of the European Miocene (von der Brelie, 1967). But the splitting of such broadly circumscribed form species into new taxa creates further problems. For instance, in the Derbyshire material alone, there are perhaps seven or eight slightly different pollen types which are all covered by Thomson & Pflug's diagnosis for *T. microhenrici*. The differences are indeed very slight, but they might be regarded as features warranting specific separation by a neopalynologist. Other European deposits have material assignable to this same form species which also shows a comparable range of variation. The creation of new species for each of these different types would produce quite an unworkable conglomeration of taxa ; it is unlikely that palynological techniques are sensitive enough to ensure adequate distinction, so they would have little practical significance either to the botanist or to the stratigrapher. Broadly based form taxa of the type adopted here avoid such confusion.

In such an instance as that mentioned above, a working solution has been proposed by Hughes and Moody-Stuart (1967). They suggest three grades of comparison, for a commonly occurring spore type, to the most appropriate published diagnosis, using a prefix cf. A, cf. B, cf. C. The type mentioned above would become "cf. C *T. microhenrici*." The same authors have since suggested that these difficulties can be best overcome, when dealing with aspects of fine correlation, by abandoning the conventional Linnean system of nomenclature and substituting individual "biorecords" for specimens of separate assemblages (Hughes & Moody-Stuart, 1969). But since this present account primarily compares the Derbyshire assemblage with those previously described in Europe, this new and radical system

of palynological nomenclature is not directly relevant. For purposes of the present work no new taxa are created, and existing Neogene taxa are used and interpreted with caution, especially when comparing stratigraphic ranges.

An important factor to bear in mind in this context of describing palynological taxa is the future role of the scanning electron microscope. It is likely that when these instruments become generally available to the palynological world they will encourage a more accurate and reliable specific diagnosis for both extant and fossil material. In the interim therefore, this gives further reason to reduce the formation of new taxa to an absolute minimum.

In describing this Derbyshire assemblage then, no palynomorphs have been identified as an extant genus together with either an extant or fossil specific epithet. Such names have often been used in the Tertiary however, for instance by Macko (1957) and Traverse (1955) respectively. It is hazardous enough to assign Tertiary pollen and spores to a modern genus; this view is evidently held by many workers using form taxa right up to the Pleistocene. Assuming that many modern species did exist in say the European Miocene, it is unlikely that the characters defining all their pollen and spores are distinctive enough to allow separation at the specific level. Reference material of all modern species of the genera which are known from macrofossils to have occurred in the European Tertiary is not available to many palynologists; and if it were it is unlikely that light microscope techniques are accurate enough to ensure uncontroversial identification of each species. But the premise, that modern species did exist in the European Miocene, is unacceptable to many. The macrofossil record (see for example Nĕmejc, 1968, and *in press*) suggests that few modern species were present in the whole of the European Tertiary. There seems to be little justification therefore to identify Neogene palynomorphs in terms of extant species of extant genera. In assigning fossil species to modern genera, Traverse (1955) made the assumption that gametophytic characters in angiosperm and gymnosperm genera can be used as a basis for erecting new plant species names in the same way as plant taxonomists use the sporophyte characters of modern plants. The method seems to have been adopted rarely in Europe, and so need not be further considered in the context of comparing members of the Derbyshire assemblage with their geographical neighbours.

Most systems of classification for fossil spores and pollen are purely morphographic, with no reference to the botanical affinities of the organisms concerned. That of Thomson & Pflug (1953) for instance, was established with the view of incorporating Neogene material just as well as forms from the Mesozoic or Palaeozoic. Few authors of Neogene palynology have ever used these systems, though there are some exceptions for Miocene work (e.g. Mazancova, 1962). Two other morphographic systems are of special interest to Tertiary workers. Van der Hammen's (1956) is based on taxa typified in terms of the spores or pollen of extant species. For example, he typifies the form genus *Monocolpites* on the type specimen *Orthrosanthus chimboracensis* (Iridaceae). Monocotyledon pollen then is the type material for a genus which is also used for fossil gymnosperm pollen e.g. *Sciadopitys*. Another system adopted by Krutzsch (1957) and later by Sonntag (1966) created 125 morphological units termed form-groups, selected for their stratigraphic unity within the Tertiary.

The components of each group are quite diverse, especially botanically, though systematic subdivision of each group has not been attempted.

Since, in the European Neogene, it is possible to relate nearly all pollen and spores to a botanical family, the Neogene/Paleogene boundary may be taken as the level above which the purely morphographic system can be replaced with some system based on botanical systematics. In order to include those forms which cannot be assigned reliably to a family, as is the case with some form species, they are either placed in "*Incertae Sedis*" (Traverse, 1955 ; Rouse, 1957 ; Pons, 1964 ; Couper, 1953) or else the most eligible family is shown as a heading preceded by a question mark (Potonié et al., 1950 ; Doktorowicz-Hrebicka, 1957 ; Pacłtova, 1963). For purposes of continuity within the systematic part of this paper, this latter method will be adopted here, subdivided by both form genera and species, or else by modern genera alone.

Several difficulties with this system do arise however. Some Neogene form species cannot be assigned (from comparison of the fossil type with Recent material) with certainty to any botanical family. For instance in the case of *Tricolpopollenites ipilensis* Pacłtova, a similar pollen type is found in modern members of both the Leguminosae and the Salicaceae. In the system of classification used here, the question marks are very important. But it is hoped that the resulting layout is conformable with the International Code, and will avoid the problems that occur in systems which have a morphographic "addenda" or which incorporate the botanical affinity in the form generic name (Rouse, 1957).

Another difficulty arises from different opinions concerning the role of the form-species : some have advocated recognition of large broadly defined units, while others favour small ones with very precise diagnoses. These two opposing views are supported by, among others, Skarby and Krutzsch respectively. Krutzsch's method of morphological description involves very accurate measurement so creating large numbers of new taxa, whilst Skarby's species have synonymy with many taxa of other authors and cover wide stratigraphic ranges. *Gleicheniidites senonicus* Ross, as emended by Skarby (1964) extends from Jurassic to Pliocene deposits and has synonymy with 37 previously cited taxa. Both extremes however are able to convey accurate information : at the risk of being considered hypocritical, I adopt both practices in the systematic part of this paper.

Arguments in response to the present high output of new taxa are well known. On the one hand (Hughes & Moody-Stuart, 1967) we are advised to consolidate within the present taxa, so that few more new species need be made, at least by the Linnean system. Whilst on the other hand (Faegri et al., 1967), encouragement is given to "propose new artificial taxa" in "cases of uncertain identification . . . involving loose or inexact" comparison. It is hoped that this paper will show that this latter view is not necessarily applicable to European Neogene palynology, at least.

III. METHODS

Pollen preparations have been made by macerating 1 c.c. samples of plant bearing clay in hydrofluoric acid in the cold, for up to four hours. The residue was shaken in

10% hydrochloric acid, centrifuged, and the sediment then floated in zinc bromide solution (specific gravity 1.9). Especial care was taken in the preparation of the series of macerations used to determine the Absolute Pollen Frequency (see Section 5). Equal weights to the nearest milligram of air dried sample were macerated, each in precisely the same way, with the addition of equal volumes of reagents to each sample. To ensure that an equal volume of suspension was evenly distributed under the coverslip of each preparation, the pollen counts were checked by the use of a haemocytometer.

The preparations of all the palynomorphs figured in this paper are deposited in the British Museum (Natural History), together with a representative range of clay samples. Although the Derbyshire exposures referred to in Section V are exposed at the date of going to press, plans of the Bee's Nest pit owners are underway to remove the plant bearing bed in the near future.

A reference collection has been prepared of pollen and spores from Recent species of most of the genera mentioned in Section IV. Many authors (Traverse, 1955; Faegri & Iversen, 1964) stress the importance of such a collection to those engaged in Tertiary palynology, especially as an aid to identification. But since there is great variation in pollen morphology within most genera found in the Derbyshire flora, the collection was found to be of little use in identification beyond the generic level. Of comparable value to this modern pollen reference collection is the comparative reference material from Neogene deposits of West Germany, East Germany and Czechoslovakia. When used in conjunction with the published descriptions of the deposits concerned, such comparison was found to be of great value for purposes of identification. The view is presented in Section VI that in the Lower Pliocene of Europe, the vegetation is likely to have been made up of very few species that frequent Europe today. So to obtain full benefit from Recent comparative material it is necessary to refer to pollen from every living species of each genus—a very exacting task.

IV. SYSTEMATIC PART

Each of the 63 taxa which have been identified from the Derbyshire material (listed in Table 1) are discussed in this section. They are arranged under the heading of their botanical family, and where this is in doubt, the family name is followed by a question mark.

TABLE 1

List of the pollen and spore taxa which have been identified within the Derbyshire assemblage.

SPHAGNACEAE

1. *Stereisporites* (*Stereisporites*) *minor microstereis* Kr.
2. *S.* (*Stereisp.*) *stereoides stereoides* (R. Pot. & Ven.)
Th. & Pf.
3. *S.* (*Distancoraesporis*) *crucis* Kr.
4. *S.* (*Distanc.*) *wehningensis* Kr.
5. *S.* (*Distanc.*) *germanicus rhenanus* Kr.
6. *S.* (*Distverrusporis*) *pliocenicus pliocenicus* Kr.

7. *S. (Distgranisporis) minimoides* Kr.
 8. *S. (Distgran.) granisteroides* Kr.
 9. *S. (Stereigranisporis) semigranulus* Kr.
 10. *S. (Stereigran.) magnoides* Kr.
 11. *S. (Distzonosporis) microzonales* Kr.
 12. *Lycopodium* sp.
 LYCOPODIACEAE
 GLEICHENIACEAE
 OSMUNDACEAE
 POLYPODIACEAE
 13. *Gleicheniidites senonicus* Ross, emended Skarby
 14. *Osmunda* sp.
 15. *Laevigatosporites haardti* (R. Pot. & Ven.) Th. & Pf.
 16. *Verrucatosporites favus* (R. Pot.) Th. & Pf.
 SCHIZAEACEAE ?/
 POLYPODIACEAE ?
 17. *Leiotriletes wolffi* Kr.
 18. *L. wolffi brevis* Kr.
 19. *Triplanosporites microsinuosus* Pf.
 TAXODIACEAE
 20. *Inaperturopollenites hiatus* (R. Pot.) Th. & Pf.
 21. *I. dubius* (R. Pot.) Th. & Pf.
 22. *Cryptomeria* sp.
 23. *Sciadopitys* sp.
 PINACEAE
 24. *Abies* sp.
 25. *Cedrus* sp.
 26. *Keteleeria* sp.
 27. *Picea* sp.
 28. *Pinus sylvestris*-type
 29. *P. haploxylon*-type
 30. *Tsuga canadensis*-type
 31. *T. diversifolia*-type
 32. *Podocarpoidites libellus* R. Pot.
 PODOCARPACEAE ?
 PAPILIONACEAE ?
 33. *Tricolpopollenites ipilensis* Paclt.
 34. *T. liblarensis fallax* (R. Pot.) Th. & Pf.
 35. *T. liblarensis liblarensis* (Th.) Th. & Pf.
 SYMPLOCACEAE
 36. *Porocolpopollenites rotundus* (R. Pot.) Th. & Pf.
 37. *P. vestibulum* (R. Pot.) Th. & Pf.
 NYSSACEAE
 38. *Nyssa* sp.
 ARALIACEAE
 39. *Hedera* sp.
 40. *Tricolporopollenites edmundi* (R. Pot.) Th. & Pf.
 HAMAMELIDACEAE
 41. *Liquidambar* sp.
 SALICACEAE
 42. *Salix* sp.
 43. *Tricolpopollenites retiformis* (R. Pot.) Th. & Pf.
 MYRICACEAE
 44. *Myrica* sp.
 BETULACEAE
 45. *Alnus* sp.
 46. *Trivestibulopollenites betuloides* Th. & Pf.
 FAGACEAE
 47. *Tricolpopollenites microhenrici* (R. Pot.) Th. & Pf.
 CORYLACEAE
 48. *Corylus* sp.
 49. *Carpinus* sp.
 JUGLANDACEAE
 50. *Juglans* sp.
 51. *Carya* sp.

ULMACEAE	52. <i>Ulmus</i> sp.
AQUIFOLIACEAE	53. <i>Tricolporopollenites iliacus</i> (R. Pot.) Th. & Pf.
	54. <i>T. margaritatus</i> (R. Pot.) Th. & Pf.
SAPOTACEAE	55. <i>Tetracolporopollenites sapotoides</i> Th. & Pf.
ERICACEAE	56. <i>Empetrum</i> sp.
	57. <i>Calluna</i> sp.
	58. <i>Erica</i> sp. ?
	59. <i>Rhododendron</i> sp. ?
ONAGRACEAE	60. <i>Corsiniipollenites maii</i> Kr.
COMPOSITAE	61. <i>Compositoipollenites rizophorus</i> R. Pot.
LILIACEAE	62. <i>Periporopollenites echinatus</i> (Wode.) Th. & Pf.
GRAMINAE	63. <i>Graminidites media</i> Cookson.

SPHAGNACEAE

1. *Stereisporites* (*Stereisporites*) *minor microstereis* Kr.
2. *S. (St.) stereioides stereoides* (R. Pot. & Ven.) Th. & Pf.
3. *S. (Distancoraesporis) crucis* Kr.
4. *S. (Distanc.) wehningensis* Kr.
5. *S. (Distanc.) germanicus rhenanus* Kr.
6. *S. (Distverrusporis) pliogenicus pliogenicus* Kr.
7. *S. (Distgranisporis) minimoides* Kr.
8. *S. (Distgran.) granisteroides* Kr.
9. *S. (Stereigranisporis) semigranulus* Kr.
10. *S. (Stereigran.) magnoides* Kr.
11. *S. (Distzonosporis) microzonales* Kr.

(Pl. I, Figs. I-11)

Spores assigned to this family are very commonly found throughout the whole European Tertiary. Many authors are in the habit of assigning them to *Sphagnum* sp. despite the lack of any supporting evidence from macrofossils that this genus commonly existed in the Tertiary. The spores are indeed comparable with those of the extant genus but it is hard to prove specific identity with any of the present British species (Tallis, 1962). The only Tertiary macrofossil remains from Europe, though without spores *in situ*, are described from the Miocene of Willershausen (Straus, 1952) and Upper Silesia (Szafer, 1961), and these do not compare closely with any living species.

Krutzsch's Atlas (1963b) describes no fewer than 64 form species of the form genus *Stereisporites*, which he regards as having affinity with the modern genus *Sphagnum*. The form genus was originally diagnosed by Thomson and Pflug (1953) who recognized three form species, though Potonié and Venitz (1934) described *Sporites stereoides* which remains the type species of the new form genus. Krutzsch divides the taxon into seven form sub-genera on the basis of the type of distal differentiation, the presence of granulate sculpturing, and the presence of a cingulum. By their very

nature as artificial form species, and on occasions as form sub-species, there can be no reliable estimate of the number of once living species that they represent.

The spore walls of the Sphagnaceae seem to have rather unusual properties. In Recent material the mature spores take up safrannin stain less effectively than immature ones. In fossil material they seem to be less well preserved than other spore types. Severe maceration has also been found to effect them more than most vascular plant spores, it often having the effect of changing the morphological characteristics to produce a spore which is immediately recognizable as one which has been so treated. Within the eleven species identified from the Derbyshire material, six form sub-genera are represented ; controversial identification is thereby reduced.

In his Atlas, Krutzsch cites a "stratum typicum" for each form species : those found in the Derbyshire assemblage fit this intimation of age very well. This however, does not mean that Krutzsch's stratigraphic observations are to be regarded as the concise ranges for each type. Other authors have attached no such significance to the use of spores from this family as stratigraphic markers, the range of the family in Europe being from the Jurassic to the present.

LYCOPODIACEAE

12. *Lycopodium* sp.

(Pl. 2, Fig. 1)

Apart from variation in the shape in outline from round to triangular, there seems to be complete morphological uniformity in all the *Lycopodium* specimens found in both Derbyshire localities. Examination of spore macerations of the modern species *L. clavatum* show a similar variation in shape. The species found here differs from this modern British species in having fewer, though larger, reticulum meshes.

Since there has been just one species found here, and since the morphology of *Lycopodium* spores seems to be distinctive for the genus, the extant generic name is used. *Reticulatisporites* (Ibrahim, 1933 emend. Pot. & Kr., 1955) includes many species with reticulum meshes of larger size than the extant European species of *Lycopodium*, in the same way as the Derbyshire specimens ; but in the Tertiary, this form genus is usually assigned to *Lycopodium* sp.

Krutzsch (1963, a) gives a comprehensive review of twenty nine form genera which can be assigned to the Lycopods, whilst making new combinations for all lycopodiaceous spores to *Retitriletes* (van der Hammen, 1956, emend. Krutzsch, 1963, a), *Camarozonosporites* (Pant, ex. Pot. 1956), or *Selagosporis* (Krutzsch, 1963, a). The Derbyshire species closely resembles *Retitriletes rueterbergensis* (Krutzsch, 1963, a), and also a figured specimen which Mazancova (1962) refers to *Reticulatisporites potonie* Th. & Pf., though these two taxa are not synonymous. This particular conflict demonstrates the confusion that has been caused by the creation of so many taxa for this family ; it is most likely that many species have been based on features of preservation.

GLEICHENIACEAE

13. *Gleicheniidites senonicus* Ross, emended Skarby

(Pl. 2, Fig. 2)

The recognition of spores from this family is both a complex and controversial matter, mainly as a result of difficulties in interpreting the three dimensional spore morphology as seen by the light microscope. Bolchovitina (1967) proposed the use of four form-genera within the Gleicheniaceae, each differing in characters of the equatorial thickening, corner projections, or sculpturing. The Derbyshire specimens are assignable to one of these form-genera, *Gleicheniidites* (Ross, 1949) as *G. senonicus*, the type species having been recently revised by Skarby (1964).

The Derbyshire spores, as well as other gleichenioid types described by Thomson and Pflug (1953) and Krutzsch (1959) often show a feature that has been referred to as a "torus"; indeed, Krutzsch makes use of variation in this feature when separating new sub-form-genera within *Gleicheniidites*. Skarby however points out that the structures described by these authors are not tori in a morphological sense, but rather phenomena resulting from optical sections of the inwardly curving wall. Skarby's conclusion is that the outer part of the wall of *G. senonicus* is completely smooth, and she has made comparable observations of this from material of Krutzsch's *Neogenisporis neogenicus* and Thomson and Pflug's *Concavisporites acutus*, *C. argulatus* and *C. obtusangulus*. All these form-species she has placed in synonymy with *Gleicheniidites senonicus*, and this is accepted here.

There is great range in both the size and shape of the "torus" in the specimens of *G. senonicus* which have been examined from Derbyshire, and often it is completely absent. This variation could be due to the spore's orientation, or even to the degree of compression.

Thomson and Pflug (1953) and Krutzsch (1959) both stress that their gleichenioid spores are important Mesozoic—Lower Tertiary index fossils. Krutzsch however, has described two occurrences of spores, now assigned to *G. senonicus*, from the Neogene. One is from the Miocene at Leipsch (*Neogenisporis neogenicus* Kr. 1962) and the other from the Pliocene at Rüterberg (originally *Cingulatisporites pseudoneddeni* Kr. 1959; then included in *N. neogenicus* Kr. 1962). This Derbyshire record gives support to Skarby's claim that *G. senonicus* ranges in Europe from the Jurassic to the Pliocene. Though the modern species of the family now occupy mainly tropical environments, a few species do occur in the southern temperate zone of Europe. If the Pliocene plant was at all similar to those of the modern genera of the family, the climate in Pliocene Derbyshire must have been frost-free.

OSMUNDACEAE

14. *Osmunda* sp.

(Pl. 2, Fig. 3)

Spores from this family have been referred to the modern species more readily than most other pollen and spore types found in the Neogene. Zagwijn (1960) and Pons

(1964) for instance both distinguish between *Osmunda regalis* and *O. claytoniana* : the latter having been previously described from the Polish Pliocene (Szafer 1954). Comparisons of fossil specimens have also been made to the extant *O. javanica* and *O. regalis* by Leschik (1951) and also Neuy-Stolz (1958). Morphological similarities led Leschik to set up *O. regloide*-type and *O. javonicoide*-type, though only the latter closely resembled the modern equivalent in size range.

Two form-genera, *Rugulatisporites* Th. & Pf., and *Baculatisporites* Th. & Pf. have been applied to spores from this family, though the latter has been compared by the original authors to *Pteridium* spores. *Rugulatisporites* was originally diagnosed as having elongate sculpturing elements, whilst *Baculatisporites* is baculate. Krutzsch (1967) however has referred the Thomson and Pflug type species for *Rugulatisporites* to the new combination *Baculatisporis quintus* which is based on the genotype *B. primarius* (Wolff, 1934) Th. & Pf.

Due to the absence of really well preserved specimens, it is not possible to assign the Derbyshire specimens to any of these form taxa.

POLYPODIACEAE

15. *Laevigatosporites haardti* (R. Pot. & Ven, 1934) Th. & Pf. 1953

16. *Verrucatosporites favus* (R. Pot., 1931) Th. & Pf. 1953

(Pl. 2, Figs. 4-6)

Laevigatosporites is the form-generic name originally proposed for smooth walled bilaterally symmetrical monolete spores, occurring from the Carboniferous to the Tertiary. Potonié (1967) assigns the form genus to Palaeozoic Sphenophyllaceae and Calamitaceae, whilst other authors accept that the Tertiary forms of the genus are from plants of the Polypodiaceae. Krutzsch (1967) divided the species into three form sub-species, differing mainly in size and shape, though all have Miocene "*stratum typicum*". *L. haardti haardti* Krutzsch is by far the most widely occurring of the three groups, and most closely resembles the Derbyshire specimens. It is found commonly in most Tertiary deposits of Europe ; Krutzsch lists many of the European Neogene occurrences in his list of synonymies.

The form genus *Verrucatosporites* was set up by Thomson and Pflug (1953) with a Tertiary type species. Potonié's original species *Polypodiisporites favus* (combined by Thomson & Pflug into *V. favus*) has been separated into four subform species by Krutzsch (1967) again mainly on differing size characters. Though perhaps commonest in the European Miocene, the species has no stratigraphic significance other than a broad Tertiary occurrence. The species closely resembles *Polypodium vulgare* which is now very widely distributed within the British Isles. This modern specific name has been used by some authors (e.g. Zagwijn, 1960) to describe Pliocene material.

SCHIZAEACEAE ? or POLYPODIACEAE ?

17. *Leiotriletes wolffi* Kr.
18. *L. wolffi brevis* Kr.
19. *Triplanosporites microsinuosus* Pflanzl

(Pl. 2, Figs. 7-9)

The two subspecies of *Leiotriletes wolffi* set up by Krutzsch (1962) fit precisely two spore types occasionally found in the Derbyshire assemblage. Krutzsch describes specimens of both form-subspecies from the German Miocene and Pliocene, but avoids relating them to any botanical family. Comparison with spores from modern *Lygodium* and *Pteridium* species shows similarity to both fossil types, but little to distinguish one genus from the other. Confirming these observations, Thomson & Pflug (1953) suggest affinity to both these extant genera for their Tertiary species of the form-genus *Laevigatisporites* which Krutzsch has combined into the form-genus *Leiotriletes*, adding to it several completely new species which occur in the Miocene and Pliocene. Both smooth walled schizaeaceous spores and the indistinguishable polypodiaceous types have been referred to other form-genera, such as *Lygodium-sporites* (R. Pot. & Gell., 1933) emend. R. Pot. 1956, and *Toroisporitis* Krutzsch, 1959. In his monograph on spores of the genus *Schizaea*, Selling (1944) shows morphological types including the smooth walled and rugulate monolete forms, little different to those commonly assigned to *Polypodium* sp.

Apart from rather dubious records of *Lygodium* from the Pliocene of southern France (Pons, 1964), and *Schizaea* cf. *pusilla* (see Potonié, 1967) from the Pliocene of Rüterberg (Krutzsch, 1959), Krutzsch's (1962) records of *Leiotriletes wolffi* and *Toroisporitis* ? *pliocaenicus* are the only other specimens of this *Lygodium*-like spore to have been described from strata more recent than the Miocene in Europe. Krutzsch (1957) himself previously recognized spores of this kind (form groups 13, 14 and 15) from the Cretaceous up only to the middle Miocene. The macrofossil record gives no evidence of any Schizaeaceous genus being present in Europe later than the record from the Lower Miocene of Germany by Kräusel & Weyland (see Gothan & Weyland, 1964, p. 203). In the Dorset and Hampshire Paleocene, Chandler (1955) described fertile material with spores of this type from species of *Aneimia* and *Lygodium*; but five genera of the Polypodiaceae were present as macrofossils in the Bournemouth Beds. This family occurs again in Britain in the Ludham borehole (= Tiglian) as *Pteridium aquilinum* (West, 1961). The Derbyshire record then, could either represent an intermediate of the Polypodiaceae (*Pteridium*) record through the Tertiary into the Pleistocene, or else mark one of the last occurrences of *Lygodium* in Europe.

Grebe (1953) has suggested that *Lygodium* is a pioneer plant following forest fire. In the Miocene German browncoals the spores of the genus are most commonly found on top of fusinite layers of coal, itself a product of such fires. Some of the macrofossil material found in the Bee's Nest pit has a type of preservation which suggests that forest fires occurred in Derbyshire during the formation of the deposit.

Triplanosporites microsinuosus Pflanzl is shown by Krutzsch (1967) to occur from the Oligocene to the Pliocene in Germany. Potonié (1967) suggests that this whole

form-genus might be assigned to either the Schizaeaceae or else to the Dipteridaceae or Dicksoniaceae.

TAXODIACEAE

20. *Inaperturopollenites hiatus* (R. Pot.) Th. & Pf.
21. *I. dubius* (R. Pot.) Th. & Pf.
22. *Cryptomeria* sp.
23. *Sciadopitys* sp.

(Pl. 3, Figs. 1-4)

Previous authors of works on Tertiary palynology have described pollen of the Taxodiaceae (exclusive of *Sciadopitys*), in one of three ways. Doktorowicz-Hrebicka (1959) and Osztas (1960) explain features which make it possible to distinguish Neogene papillate pollen at the generic level, though implying that broken or gaping taxodiaceous pollen is not identifiable in this way. Zagwijn (1960) used just two groups, *Taxodium*-type (cf. *Taxodium* and *Glyptostrobus*) and *Sequoia*-type (cf. *Sequoia*, *Cryptomeria* and *Metasequoia*) with small and large papillae respectively. He made no further distinction at the generic level, and included all gaping forms without papillae in the group *Varia*. Pons (1964) adopted these same two divisions, but made tentative suggestions at generic identification within each group. Other authors approve of the advice given by Potonié (1967) that separation of taxodiaceous (excluding *Sciadopitys*) pollen is not at all reliable at the modern generic level; consequently, the use of form taxa is preferable to the use of modern generic names.

Of these controversial taxodiaceous forms, three types occur in the Derbyshire assemblage. They are all present in very low frequencies, in contrast to the situation in the majority of West European Pliocene deposits where they form a major component of the pollen assemblages. Specimens of papillate forms occur, though very rarely, and are assigned to *Cryptomeria* sp. on account of their long curved papilla—a character of pollen from this genus mentioned by Doktorowicz-Hrebicka. The occurrence of macrofossil *Cryptomeria* in the same Derbyshire deposit gives further support to this identification (Boulter, *in press*). Two forms of gaping taxodiaceous pollen also occur, but the papillae are never visible. Examination of modern material shows that the pollen grains begin to split open along the axis of the papilla, so that when gaping fully open, the papilla is quite unrecognizable. *Inaperturopollenites dubius* is a form species for one such gaping type. It has a relatively thin exine, not exceeding $0.5\ \mu$ in thickness, and often has secondary folds. The exine is very finely intrapunctate, and the grain is always oval in shape. Spores of modern *Equisetum* are very similar to this form, but since no elaters have been found in any of the preparations, the possibility of its occurrence is felt to be remote. *Inaperturopollenites hiatus* has a thicker (more than $0.5\ \mu$) smooth exine, and is always spherical in outline.

Sciadopitys pollen is monocolpate and coarsely verrucate, quite distinctive enough to make the form name *Monocolpopollenites serratus* (R. Pot. & Ven.) Th. & Pf. unnecessary in this case, especially since there are macrofossil remains of *Sciadopitys*

tertiaria leaves in the same Derbyshire deposit. Although *Sciadopitys* pollen has been recorded as high as the Tiglian, it is rarely so abundant as in this assemblage. Only at a few sites (von der Brelie, 1959, p. 34) does it exceed 10% of the total pollen count, the genus having gradually diminished in significance since the time of deposition of the *Sciadopitys* Graskohle during the Miocene.

PINACEAE

24. *Abies* sp.
25. *Cedrus* sp.
26. *Keteleeria* sp.
27. *Picea* sp.
28. *Pinus sylvestris*-type
29. *P. haploxylon*-type
30. *Tsuga canadensis*-type
31. *T. diversifolia*-type

Abies sp.

(Pl. 3, Fig. 5)

This pollen has been differentiated from that of *Keteleeria* occurring in this assemblage by reference to the thickness of the exine at the proximal face of the corpus. In specimens of *Abies*, this measures about 10 μ , whilst the corpus of *Keteleeria* pollen has proximal exine no thicker than 4 μ . The sculpturing elements are so similar that they have not been used to separate the pollen from the two genera. Indeed, Zagwijn (1960) did not separate them at all, whilst others who have done so rarely give full justification, as explained by Ferguson (1967, p. 85).

The genus has been commonly reported from more than one of the British interglacials, though specific identification has not proved possible. However, the genus was not identified from either the Ludham borehole (= Tiglian) or from any of the investigations on the lower Tertiary floras of southern England. Its occurrence in Derbyshire, both as pollen and leaf material, is the sole record of the genus in the whole of the British Tertiary, though it was extremely widespread on the continent of Europe during this time.

Cedrus sp.

(Pl. 3, Fig. 6)

The sacchi of these pollen grains are usually in the contracted position, but the pollen is best identified by the marginal crest on the proximal part of the sacchi, which continue onto the edge of the corpus. Despite its absence in the British Pleistocene, the occurrence of the genus in the Derbyshire Pliocene is not surprising. Its pollen has previously been found in the lower Tertiary deposits of southern England (Pallot, 1961) and Scotland (Simpson, 1961) whilst on the European continent, Neogene and Pleistocene records trace its restriction into present day northern Africa and the Middle East. This migration is well shown in a series of maps reproduced by

Ferguson (1967). The present record marks its most northerly known occurrence since the Paleogene, due no doubt, to the high oceanicity of the climate in west Europe, a factor which is evidently still important in the distribution of *Cedrus libani*. Comparable Pliocene records are made by Potonié et al. (1950) from Wallensen, and its occurrence in the same area is recorded by Kremp (1950) from the browncoals. The form found at Wallensen has been described by Thomson & Pflug (1953) as *Pityosporites cedroides*, a name used since by Mazancova (1962) for her Miocene material from Bohemia. This is indistinguishable from the Derbyshire specimens.

Keteleeria sp.

(Pl. 3, Fig. 7)

Not only is the pollen of this genus difficult to identify, but the macrofossil remains can be easily confused with those from other members of the family. So all parts of the fossil record of *Keteleeria* must be interpreted critically. Ferguson (1967) suggested that only four published records of *Keteleeria* pollen from the whole European Tertiary are authentic; three are from the Miocene and one from the Eocene. Pollen is convincingly recorded in the Pliocene too however, by Pacltova (1963) from southern Bohemia, and by Zert (unpublished thesis, 1960) from N.E. Bohemia.

Picea sp.

(Pl. 4, Fig. 1)

The sculpturing on both sacchi and corpus of these pollen grains is finer than in any other extant bisaccate genus; there are no marginal crests to the saccus ornamentation, whilst in lateral longitudinal view, the edge of the sacchi form a smooth curve with the edge of the corpus. The longest axis is 70–90 μ .

Both macrofossils and pollen from the genus have been commonly found in the European Tertiary and Pleistocene. In the Neogene, where Thomson & Pflug's name *Pityosporites alatus* is rarely used, there are many instances of more than one species of *Picea*. In the German Miocene, Potonié et al. (1950) illustrate a *Picea* pollen as well as a smaller "*Picea omorikoide*-type". In the Pliocene, Pons (1964) makes comparisons of three different types with living species, whilst Zagwijn (1960) distinguished between a large form corresponding to *Pityosporites alatus* and a smaller one about the size of *Pinus* pollen. A smaller type may also occur in the Derbyshire material, though its rare occurrence and similarity, especially in polar view, to *Pinus haploxylon*-type makes it very difficult to recognise. Manum (1962) found similar difficulty in dealing with the Lower Tertiary pollen that he refers to as *Abietineae-pollenites* sp. Type A. It has, he says, affinity with either *Pinus* or *Picea*, and especially to *Pityosporites microalatus* f. *major* (R. Pot.) Th. & Pf.

Pinus* haploxylon-type**Pinus* sylvestris-type**

(Pl. 4, Figs. 2-3 ; Pl. 5, Figs. 1-5)

Both these names are used in the sense that they have unknown affinity to any living species of the genus. It is unfortunate that *Haploxylon* is one of the two subdivisions of the genus *Pinus* (see Mirov, 1967) and that the only living species indigenous to the British Isles is *P. sylvestris*. Both names were originally used with just such comparative implications, but reference to pollen from living material shows that the synonymy is very insecure. For instance, Pons (1964) compared both types to pollen from several modern species but was unable to make direct synonymy. The terminology was introduced by Rudolph (1935), in one of the first major studies of European Tertiary palynology, and has never been validly diagnosed. However, the palynomorphs covered by Rudolph's terminology have been formally described and diagnosed by Potonié (see Potonié 1958 p. 61) as *Abietineaepollenites microalatus* and *Pollenites labdacus*; these specific names were subsequently assigned by Thomson & Pflug (1953) to the genus *Pityosporites*. But these form names are very rarely used in the literature; Rudolph's terminology still persists, and without proper definition, has been frequently used incorrectly. In the Neogene however, the situation is not so bad, as there is little variation from either of Rudolph's *Pinus* types. In the Paleocene and Mesozoic, the term *Pinus haploxylon* is often used without adequate regard to these facts. Ting (1969) creates a new species of *Pinus* pollen from the North American Eocene, and gives a synonymy to " = *Pinus haploxylon* Typ. RUDOLPH." Ting's figures seem to differ significantly from Rudolph's original material of the Bohemian Pliocene.

Two authors have recently helped to clarify the use and meaning of the two forms. Doktorowicz-Hrebicka (1957) and Zagwijn (1960), both interpreting Pliocene material, use the term "*Pinus haploxylon*-type" for pollen with the corpus about 40 μ in greatest diameter, in which the sacchi are attached to the corpus along a straight line and their height is the same as the corpus. *Pinus sylvestris*-type is of similar size, but the line of attachment of the sacchi to the corpus is slightly curved, and the corpus has a greater diameter than the height of the sacchi. The marginal ornamentation of the sacchi is more pronounced in this form too. Results of an experiment conducted during the course of this investigation to investigate the effect of the compression on *Pinus sylvestris* pollen show no startling results. A proportional weight of 200 m. of overburden was applied for three weeks to the modern pollen, after acetolization and suspended on a palynologically clean clay. Although the procedure initiated several secondary folds in the pollen grains, there was no dramatic change in morphology. The morphological differences between the two forms of *Pinus* pollen seem to be due to morphological differentiation.

Re-examination of new macerations from Rudolph's original localities at Neudorf and Fonsau (now named Nová Ves and Vonsov, respectively) in the Cheb basin of northeastern Bohemia supports the interpretation mentioned above to distinguish between the two types of *Pinus* pollen. Both in the Czech material and in that from Derbyshire however, there appears to be at least two forms of *Pinus haploxylon*-type.

This confirms Potonié's (1951) division of the species into two subform-species, *major* and *minor*, which were later considered and illustrated by Thomson & Pflug (1953) as *Pityosporites microalatus* f. *major* and f. *minor*. Potonié et al. (1950) also made a distinction between small and large specimens of *Pinus sylvestris*-type. This distinction of both *Pinus* types into *major* and *minor* is solely a consequence of their size difference. It could be the result of developmental factors just as much as taxonomic ones, though the apparant absence of both *minor* types from European Miocene assemblages suggest that there is some taxonomic difference.

Previous authors of Tertiary palynology have never treated *Pinus* haploxylon-type as an important stratigraphic marker ; indeed, it is regularly distributed within the Neogene and Pleistocene (see Rankama, 1967). A review of the European literature however shows that the quantitative relationship between *P. haploxylon*-type and *P. sylvestris*-type is of significance when comparing the Upper Pliocene to the Miocene. The Upper Pliocene records which distinguish quantitatively between the two *Pinus* types all show that *P. sylvestris*-type is dominant to *P. haploxylon*-type, (Zagwijn, 1960 ; Pons, 1964 ; Leschik, 1951 ; etc.). Althenger (1959) shows details of the proportions of the two *Pinus* forms from several German Pliocene localities. Only at localities believed to represent the lower part of the Pliocene, at Sylt, Ptolemais, Schosnitz and Wallensen, does the number of *P. haploxylon*-type pollen grains counted exceed the number of *P. sylvestris*-type. The smaller number of records from the Miocene show that although *P. sylvestris*-type can occasionally be dominant (Doktorowicz-Hrebnicka, 1957), *P. haploxylon*-type is itself most often dominant (Mazancova, 1962 ; Kremp, 1950 ; Oszast, 1960). Results from the Derbyshire assemblage pollen counts show that *P. haploxylon*-type is always dominant. As will be discussed in Section VI of this paper, this supports the Mio / Pliocene boundary age which has been attributed to the deposit.

Tsuga canadensis-type

T. diversifolia-type

(Pl. 6, Figs. 1-2)

As with the names used here to describe the two species of *Pinus* pollen, the original (and invalid) terminology of Rudolph (1935) for the two types of *Tsuga* pollen, though formally diagnosed by Thomson and Pflug (1953) as form-taxa, continues to be used in the literature. *Tsuga canadensis*-type has a narrow equatorial fringe with spinules up to 3 μ long, the whole pollen grain being up to 90 μ in diameter. It was this pollen type which Thomson and Pflug assigned to their form taxa, *Zonalapollenites viridifluminipites*, a name rarely used, perhaps for phonetic reasons. *Tsuga diversifolia*-type, described by Thomson and Pflug as *Zonalapollenites igniculus* has a more prominent equatorial fringe (up to 10 μ in width) which is deeply indented, but on average, the pollen has a smaller diameter than the other type, rarely exceeding 80 μ . Spinules are completely absent from this type.

Many attempts have been made to compare both these commonly occurring Neogene pollen forms to living species. If this were possible, then insight might be

gained on the way in which the genus has become restricted to Eastern Asia and North America. Originally, Rudolph implied that *Tsuga canadensis*-type was the same as pollen from modern *T. canadensis* which is now restricted to eastern North America, whilst the other type's affinity was to *T. diversifolia*, now occurring only in Japan. More recent palynological records (Pons, 1964) however, suggest that it is impossible to rely on these comparisons.

Szafer (1949) made a special study of this genus, instigated by the discovery of abundant macrofossil remains in the Middle Pliocene deposit at Kroscienko. He identified two species from the deposit, which are almost identical with the living *T. canadensis* and *T. caroliniana*, both modern North American species. He suggested that divergence from a primitive type occurred, perhaps during the Miocene, which gave rise to the two separate populations that are found at Kroscienko. But the two pollen types found in Derbyshire and elsewhere in the European Tertiary cannot be as closely compared to these same two living species as Szafer's macrofossils. Quite different palynological forms of the genus have been found in the North American Tertiary (Axelrod & Ting, 1960 ; Ting, 1969) suggesting that the species which have colonized Europe and the New World since the beginning of the Tertiary represent at least two distinct genetic lines.

PODOCARPACEAE ?

32. *Podocarpoidites libellus* R. Pot.

(Pl. 6, Figs. 3-4)

Although present here in small amounts, this bisaccate pollen is widely distributed in the sections studied. The corpus is thick walled with coarse wrinkles, and is less broad (30 μ) than the sacci (40 μ) which are irregularly reticulate, though this reticulum does radiate from the point of attachment with the corpus. Ting (1969) introduced the term "magnisaccate" to describe this size relation of corpus to sacci, and points out that modern magnisaccate pollen only occurs in the Podocarpaceae, never in the modern species of the genus *Pinus* that have been studied palynologically. There is some similarity however between pollen from modern *Pinus* species and that of *Podocarpus* which is of the prolate equisaccate (corpus prolate, sacci and corpus of the same height) type—a trend of parallel evolution. Such a trend might also have existed in the Tertiary with regard to the magnisaccate character, so that Ting's remark cannot be construed as demonstrating that this Derbyshire form is of the genus *Podocarpus*.

The question of the botanical affinity of this pollen type assigned to *Podocarpoidites libellus* bears on the historical distribution of the genus *Podocarpus*. Florin (1963) was of the opinion that the genus has never existed in the northern hemisphere. This view is not entirely unchallenged, especially since Dilcher's (1969) discovery of reliable *Podocarpus* leaves in the North American Eocene. But there are no other entirely irrefutable records either in North America or Europe. Mädlar's material from the German Pliocene was unfortunately destroyed during the war, and his published record of *P. kinkeli* is not entirely convincing (Ferguson, 1967). The

remaining European Tertiary examples of the genus are all of the dispersed pollen, which, as explained above, might be an extant species of *Pinus*. In Europe then, no fossil material exists which can refute Florin's contention that the genus never extended north of the Tethys. There is no other gymnosperm genus represented by pollen from the European Neogene which has no reliable macrofossil record in this area to support its identification in the dispersed pollen state.

Two form species, *Podocarpoidites libellus* and *Pityosporites podocarpoides* Th. 1958 have been described from the German Miocene. The first of these has been discussed by Potonié et al. (1950). It has a length of about $55\ \mu$ and seems to differ only in size from Thiergart's species, which has its longest axis at $75\ \mu$. The Derbyshire specimens most accurately fit Potonié's species, though the distinction between the two is very slight.

Lastly, 4-saccate pollen of the *Podocarpus* type is very common in the *Dacrycarpus* section of the modern genus. In other modern gymnosperm genera 4-saccate pollen only occurs as a rare aberrant type. Just three specimens of the 4-saccate pollen have been observed in the current investigation; the morphology is sufficiently similar to that of modern 4-saccate *Podocarpus* pollen to compare it to this family. These specimens also give a little more strength to the argument in favour of *Podocarpus* rather than an extinct *Pinus* as the modern genus of closest pollen morphology.

PAPILIONACEAE ?

33. *Tricolpopollenites ipilensis* Paclt.
34. *T. liblarensis fallax* (R. Pot.) Th. & Pf.
35. *T. liblarensis liblarensis* (Thoms.) Th. & Pf.

(Pl. 7, Figs. 1-6)

None of these tricolpate forms have been identified *in situ*, and their tentative attribution to this family is based solely on comparison to modern members of the family by previous authors.

Tricolpopollenites ipilensis has only recently been described from the L. Miocene of Slovakia (Pacltova, 1966). This pollen type has also been identified from Miocene deposits in Germany and also from the Mio / Pliocene boundary in S.E. Bohemia (Mazancova, pers. comm.) The exoexine has a thick clavate sculpturing (at a scale making it imperceptible in the Plate), the polar axis is about $20\ \mu$ in length, the outline is prolate, and the colpi do not reach closer than $4\ \mu$ to the poles.

T. liblarensis (Thiergart 1940) Th. & Pf. is common throughout the whole Tertiary period in Europe, though the subspecies *fallax*, unlike *liblarensis*, seems to occur most abundantly in the Miocene (Zagwijn, 1960). By the Pliocene both forms occur in diminishing quantity though more often than not they are completely absent (v.d. Brelië 1961). The species has three long colpi, and a thin exine with a smooth or intrareticulate hyaline wall, with a perprolate outline. The two subspecies differ firstly in size and secondly in ornamentation; *fallax* is less than $18\ \mu$ in length with a smooth wall, whilst *liblarensis* is larger, no more than $25\ \mu$ long, with a faintly intrarugulate ornamentation.

The natural affinity of both forms, presumably similar for the two types, has been variously suggested, or rather guessed. Thiergart (1940), proffered the Papilionaceae, an idea supported by several authors since. Potonié et al. (1950) suggest that in all probability it is a member of the Cupuliferae (i.e. Fagaceae), whilst Thomson and Pflug (1953) concede this point but alternatively suggest that it might belong to some herbaceous plant.

SYMPLOCACEAE

36. *Porocolpopollenites rotundus* (R. Pot.) Th. & Pf.

37. *P. vestibulum* (R. Pot.) Th. & Pf.

(Pl. 7, Figs. 7-9)

These two species of *Symplocos* pollen are distinguished mainly by their shape and ornamentation. *Porocolpopollenites rotundus* is more or less circular in outline with a smooth wall, whilst *P. vestibulum* has an amb with three concave sides and pronounced scabrate sculpturing. The sculpturing is often pronounced enough to give a spiny appearance comparable with some modern species of the genus, e.g. *S. setchuensis* (Erdtman, 1952, p. 424). This feature is not mentioned either in the descriptions of Potonié et al. (1950) or in the emended diagnosis of Thomson & Pflug (1953). Though some may consider it of sufficient importance to create a new species, Potonié's form species are used here with the knowledge that other investigators have adopted a broad definition to these existing taxa. Both fossil species have a vestibulum to the pores, which have very short colpi.

Although most abundant in the Miocene, pollen of the Symplocaceae has been reported from Pliocene deposits in Germany (v.d. Brelie, 1959; Rein, 1961), Holland (Zagwijn, 1960) and France (Pons, 1964). All three of these records show that the pollen occurs in very small quantities when present in the Pliocene, and with a morphology rather difficult to reconcile with any of the geologically older previously described species.

NYSSACEAE

38. *Nyssa* sp.

(Pl. 7, Figs. 10-11)

These prolate tricolporate pollen grains are identified by virtue of their three pores being circumscribed by caverna. The wall is smooth with no sculpturing elements and the polar axis is 20-25 μ in length. Thomson & Pflug's (1953) form species *Tricolpopollenites kruschi* is the most similar established taxa to the Derbyshire specimens, though its exine has fine intrarugulate ornamentation, a feature not observed in the Derbyshire material. Thomson & Pflug set up five subspecies of *T. kruschi* varying in the size and prominence of the intrarugulate structures, but only two of the taxa have stratigraphic importance with the Tertiary. There are very few specimens of *Nyssa* sp. pollen occurring in any of the Derbyshire deposits (only 12 such specimens have been observed), and consequently no reliable comparison to any of these subspecies can be made.

Pollen from the family occurs very commonly throughout the whole Tertiary period, but is not found in Europe after the cold period which marks the end of the Pretiglian (de Jong, 1967). The aquatic environment in which *Nyssa* now grows was not only more widespread in Europe during the Tertiary, but it is also more conducive to the production of a facies in which plant material can survive as fossil (Teichmüller & Teichmüller, 1968). These authors suggested that *Nyssa* formed a major association with *Taxodium*, to produce large areas of forest swamp, which gave rise to the autochthonous German browncoals. This situation is unlikely to have been repeated in Derbyshire, due to the absence of high pollen counts for both *Nyssa* sp. and the Taxodiaceae. As will be discussed later in Section VII, the apparent low amount of aquatic or swampy vegetation in the Derbyshire assemblage suggests that this played only a small part in the total vegetation cover of the region. Fassett (1960) points out that there are North American species of *Nyssa* which can grow on either dry or damp soils, so that there is no cause to regard the presence of that genus as indicating a swampy habitat.

ARALIACEAE

39. *Hedera* sp.

40. *Tricolporopollenites edmundi* (R. Pot.) Th. & Pf.

(Pl. 7, Figs. 12-14)

The pollen referred here to *Hedera* sp. is about 35 μ in length, elipsoid, tricolporate with caverna, and with reticulate sculpturing which is much finer at the poles than the equator. Tricolporate pollen of this reticulate type is very widely variable both as the dispersed fossil, and in material from a single modern species. It is likely that some of the forms regarded here as belonging to the genus *Hedera*, are members of quite a different group. But they are small in number in this deposit (as in all European Pliocene deposits) and are not thought to belong to important arboreal species. Thomson & Pflug (1953) described a baculate tricolporate form with affinity to *Hedera* as *Tricolporopollenites wallensenensis*. The Derbyshire specimens of *Hedera* sp. are not baculate; indeed, Althenger (1959) reports a conversation with Thomson in which the latter concedes that *T. wallensenensis* might belong to some other genus within the Araliaceae. Certainly all species of *Hedera* pollen examined by the author are reticulate rather than baculate.

The genus has only once been recorded in Europe from strata older than Pliocene (Pacltova, 1966). In the Pliocene itself, Althenger (1959) records at least four localities in the Upper Pliocene of Germany with reticulate pollen of *Hedera*, whilst Pacltova (1963) has found similar types at Ledenice, Southern Bohemia. The genus is well represented in the Pleistocene from several interglacials. Godwin (1956) has discussed the implications of the delicate climatic requirements of *Hedera helix*: that it cannot withstand exceptionally hard present-day British winters, when the temperature falls below -1.5°C as average for the coldest month (Iversen, 1944). This living species is consequently associated with oceanic climates in the temperate latitudes.

Tricolporopollenites edmundi can be easily identified : its most characteristic feature being the large baculae up to $3\ \mu$ in length, the entire wall being up to $8\ \mu$ in thickness. Zagwijn (1960) regards the sculpturing as clavate, occasionally merging to give an apparent negative reticulum. The species is very rare in the Derbyshire assemblage but it is nevertheless of considerable stratigraphic significance. The form is typical of European Miocene deposits (Potonié, 1967), though it occurs also in the Oligocene and the Lower Pliocene. Zagwijn (1960) has found regular though very small quantities in the Susterian and Branssumian of Holland, and Mazancova (pers. comm.) has similar quantities in her Mio / Pliocene assemblage from Jihlava, S.E. Bohemia. Pons (1964) records the species from the most recent Pliocene deposits (Middle / Upper Pliocene) of La Bégude and Mollon-Ravin in southern France, though this of course is more than 1,000 Kms. south of these other records in Holland and Derbyshire, which may be correlated with its higher stratigraphic position. The absence of this pollen type from Upper Pliocene deposits of Central and Western Europe provides further support for a Lower Pliocene age to the Derbyshire Flora. In an extensive comparison of this fossil pollen with that from modern material, Mamczar (1962) has concluded that *T. edmundi* shows greatest resemblance to pollen from the genus *Aralia*.

HAMAMELIDACEAE

41. *Liquidambar* sp.

(Pl. 8, Fig. 1)

This pollen, similar to that described by some authors as *Periporopollenites stigmosus* (R. Pot.) Th. & Pf., is about $40\ \mu$ in diameter, and the exine is intrarugulate with distinct though very small columellae. More recently, Krutzsch (1966) has submitted a revised diagnosis of this form species based on the structure of the pores, and corresponding well to the Derbyshire material. Pollen, described as either *P. stigmosus* or *Liquidambar* sp., has been commonly identified from the whole Tertiary of Europe, and has been well reviewed by Potonié (1967). The genus did not return to northern and central Europe after the first cold period of the Pretiglian following in this respect the behaviour of the taxodiaceous genera and *Nyssa*, with which *Liquidambar* is regularly associated in modern environments.

Kouprianova (1960) has traced the palynological history of the modern genus right back to the Cretaceous. She has identified four of the modern species from Miocene or Oligocene deposits and has suggested that recognizable fossil species have linked these four to an original subtropical member of the genus from which all these other species evolved. However, there is no reference in her scheme to the pollen type present here. Thomson & Pflug's form species is not so narrowly defined as are Kouprianova's species ; indeed, *P. stigmosus* could well be synonymous with all the species that Kouprianova mentions. But implications do arise from the ecological associations of both the modern species of *Liquidambar* and of Kouprianova's species. *L. formosana* and *L. macrophylla* both grow in the far east with genera such as *Pinus*, *Cryptomeria*, *Tsuga* and *Quercus* ; plants which are present in the Derbyshire fossil

assemblage. *Liquidambar angaridae* Kouprianova from the Lower Oligocene of Western Siberia is also a member of a similar group of plants to those represented in the Derbyshire assemblage.

SALICACEAE

42. *Salix* sp.

43. *Tricolpopollenites retiformis* Th. & Pf.

(Pl. 8, Figs. 2-3)

The "salicoid" pollen of the European Tertiary is so diverse, especially in the nature of the exine ornamentation, that there are likely to be numerous genera and species represented, not necessarily of this family. The pollen referred here to *Salix* sp. is finely reticulate, each lumen being about $1\ \mu$ in length. This form is comparable to the "Salicoid" form mentioned by Zagwijn (1960) from the Dutch Pliocene (verbal comm.). Apart from his record, the type is difficult to trace in accounts from other Neogene deposits, due to the close similarity of so many tricolpate forms of this size (about $25\ \mu$ long, prolate). For instance, it is often difficult, especially when preservation is bad, to distinguish between this form with very fine reticulation and other intrabaculate forms assigned to *T. microhenrici*. Certainly it is difficult to point to any differences between the Derbyshire *Salix* sp. type and certain of Thomson and Pflug's (1953) illustrations of *T. microhenrici*.

The other pollen type assigned to the Salicaceae corresponds to the form species *Tricolpopollenites retiformis*. Thomson & Pflug (1953) suggested that its botanical affinity was to either the Salicaceae or the Platanaceae, though subsequent assignments have been made solely to the former family. This tricolpate pollen is up to $35\ \mu$ in length and has a baculate surface with an extremely thin nexine. Widespread variation in the size of the baculae is common not only in the English material but also in that from Germany and elsewhere. Though distinct from the form referred here to *Salix* sp., other authors have used this modern generic name to describe pollen indistinguishable from that of *T. retiformis* (Pons, 1964 ; Leschik 1954 ; Neuy-Stolz, 1958 ; Pacltova, 1963). At least the baculate form seems to have been more widely distributed than the form referred here simply to *Salix* sp.

MYRICACEAE

44. *Myrica* sp.

(Pl. 8, Fig. 4)

This triporate pollen is best distinguished from other pollen with this basic morphological feature by the presence of the atrium at each pore ; that is, the area in which the endexine is absent from the pore region. This point of distinction can only rarely be used in conducting pollen counts however, as bad preservation and oblique orientation often hide the feature. Other distinguishing characters such as

size, shape and sculpturing, mentioned by Zagwijn (1960), are also regularly obscured and cannot be relied upon to make quantitative determinations in Tertiary material. But Romanowicz (1962) has produced evidence which suggests that *Myrica* pollen is more abundant in the European Neogene than any other triporate pollen. She differentiated ten forms of the genus, and compared some of these to pollen from such modern species as *M. javanica*, *M. carolinensis*, and *M. gale*.

Pollen from the genus has been regularly identified from both Neogene and Pleistocene deposits throughout Europe. The extant European species of the genus, *M. gale* (the bog myrtle), is characteristic of fens and bogs, often succeeding *Sphagnum* and *Calluna* associations. The chief genera which ecologists associate with *M. gale* in the modern environment were seemingly present in Derbyshire during the Lower Pliocene.

BETULACEAE

45. *Alnus* sp.

46. *Trivestibulopollenites betuloides* Th. & Pf.

(Pl. 8, Figs. 6-7, 9-10)

The *Alnus* pollen present in the assemblage has four or five pores with the characteristic arci connecting adjoining pores. Observations on modern species show that the number of pores varies within a single species, so that the fossil material could represent just one species. Other features vary within single species of this genus, for instance the wall thickness—a character used by Doktorowicz-Hrebicka (1964) to separate fossil remains of *Alnus* pollen into twelve “forms”. The single form species *Polyvestibulopollenites versus* (R. Pot.) Th. & Pf. has been applied to numerous specimens of the *Alnus* type pollen in the European Tertiary; pollen which seems to be identical with that from the Derbyshire deposits. Both Thomson & Pflug (1953) and Krutzsch (1957) point out that the genus was rare in Europe during the Paleogene, but increased during the Neogene to reach a maximum during the Pleistocene.

Examination of acetolysed pollen of some of the modern species of *Betula* shows little variation within the genus. The pollen is distinctive enough to assure accurate identification of the genus; triporate, with each pore protruding and distinctly vestibulate. The fossil material from Derbyshire that can be assigned in this way to *Betula* spp. has great variation in both size and shape. If the species uniformity seen in the modern pollen prevails in the Neogene material, then there are several species of the genus represented here. But there is substantial difficulty encountered even by Quaternary botanists in distinguishing between pollen of the modern British species (Birks, 1968). In the light of this possibility, the betuloid forms are here referred to by the form name *Trivestibulopollenites betuloides*. Thomson & Pflug's diagnosis allows quite a wide variation in both size and shape (“18-35 μ . Contour roundish . . .”) so as to accommodate all the forms found here. The problem has been dealt with in other ways by Tertiary workers: Doktorowicz-Hrebicka (1964) described 14 “forms” of *Betula* species, Macko (1957) compared to modern species, whilst the majority of authors have assigned the pollen to either *Betula* sp. or else to the form taxon used here.

FAGACEAE

47. *Tricolpopollenites microhenrici* (R. Pot.) Th. & Pf.

(Pl. 8, Figs. 11-13)

This important Neogene taxon was introduced by Potonié (1931) (as *Pollenites microhenrici*) who regarded the pollen as tricolporate. In their revised diagnosis, Thomson & Pflug reinterpreted the pore structures as geniculi, which they explained are often absent altogether. Indeed, geniculi are often difficult to discern even in modern pollen grains which are reputed to possess them. The significance of the geniculus (*sensu* Thomson & Pflug) in the evolution of pollen morphology has been briefly mentioned by Doyle (1969) who suggests that the presence of a geniculus represents a primitive colporate condition. *T. microhenrici* could well represent an even more primitive state in that the geniculi are not always present. Perhaps the scanning electron microscope can help to solve this problem. Before 1953, several authors used the generic name *Quercoidites* for this pollen, based on the species *henrici* which shows a geniculus (Potonié et al. 1950). In their diagnosis of the form species, *Tricolpopollenites microhenrici*, Thomson & Pflug also describe the exine ornamentation as intragranulate or intrabaculate, a character which is evident in the Derbyshire specimens.

Small tricolpate and tricolporate pollen grains are traditionally extremely difficult to identify and describe accurately, mainly because there are so few variable characters. Size, shape, exine ornamentation and length of colpi are so often the only criteria available. Consequently, many important arboreal and herbaceous genera are most difficult to identify by current palynological techniques, and most of these are represented in the extant flora by numerous species. So not only is there inevitable variation in the form of *T. microhenrici* as diagnosed by Thomson & Pflug and shown in their photographs, but also, any attempt to seek a modern botanical affinity is likely to be extremely unreliable. The Derbyshire material presents no exception to this, and it is often difficult to distinguish between the various tricolpate forms occurring in the assemblage. Although the diagnosis of *T. microhenrici* adequately describes many of the specimens from this assemblage, there is some variation especially in the shape and nature of the colpi. Indeed, some authors of Tertiary palynology would use this variation as a basis for several new species. It is also occasionally difficult to observe the nature of the exine ornamentation, so as to distinguish between this type and *T. liblarensis*.

Most authors are in agreement however, that *T. microhenrici* is most likely to have affinity with pollen of the modern genus *Quercus*. The pollen has a similar morphology to that from some modern tropical and subtropical species of the genus, and Pons (1964) has stressed similarity to the southern European species *Q. mediterranea*.

In view of the variation in the form of this tricolpate pollen type, any comparison between different authors' records, even within a limited area such as Europe, must inevitably have limitations. Pliocene records of *T. microhenrici* in Europe are very rare. Zagwijn (1960) found a very small number of this type in the Lower Pliocene deposits of Holland, whilst further south in the Rhodanienne, Pons (1964) identified

a significant percentage of pollen from four species of *Quercus*, including that which he referred to *Q. mediterranea*. Reviewing the German records of *T. microhenrici* however, von der Brelie (1967) showed that the species has never been recorded there from the Pliocene, so that it may accordingly be regarded as a consistent member of the component typical of Miocene assemblages. Other German authors too (Potonié, 1931; Thomson & Pflug, 1953) restrict the species range to Oligocene and Miocene deposits, whilst Zagwijn (1960) has found it as an abundant member of Miocene floras in Holland.

The occurrence of *T. microhenrici* in this Derbyshire assemblage of presumed Mio / Pliocene boundary age can be reconciled with the European data, especially in the light of Zagwijn's record from an approximately equivalent horizon. What is not so easy to explain in terms of this age determination however, is the large percentage occurrence of the form in the samples from the Bee's Nest pit (Fig. 5). If the Derbyshire form is identical with that from the Continent (an assumption by no means certain, as implied above when discussing the variation within the form species) then the more oceanic climate of Derbyshire during Neogene times might account for the more abundant occurrence of the type here.

CORYLACEAE

- 48. *Corylus* sp.
- 49. *Carpinus* sp.

(Pl. 8, Figs. 5 & 14)

The pollen from both these genera is very common throughout the whole Tertiary period; in Britain both have been identified palynologically from the Lower Tertiaries of southern England (Chandler, 1964) and from just a small number of Quaternary sites. *Corylus* is most easily identified by its simple germinal aperture, having no separation of the ectexine from the endexine. *Carpinus* has 3–5 pores, most commonly four, with a thin chagriniate exine. In this investigation, no attempt has been made to separate either genera into consistent species, whilst in quantitative analysis, it has often proved to be impossible to separate *Corylus* from *Myrica* due either to poor preservation at the pore region, or else to an oblique orientation of the grain in the glycerine jelly.

JUGLANDACEAE

- 50. *Juglans* sp.
- 51. *Carya* sp.

(Pl. 8, Figs. 15–16)

Juglans pollen has been recorded both from British Interglacials (Godwin, 1956) and from the Oligocene beds of S.E. England (Chandler, 1964), so its occurrence here is not surprising. Krutzsch (1957) shows that this type of pollen is most abundant in Germany in deposits of Miocene age, whilst further west in Holland, Zagwijn (1960) has recorded the genus only from Pliocene and Pleistocene strata.

The Derbyshire material is extremely rare and has up to eight sub-equatorial pores, and a diameter of about $30\ \mu$.

Carya on the other hand, has been found in Europe no higher than the Tiglian (Zagwijn, 1963) and though it occurs in the Paleogene (in small quantities) it is regarded as an important component of the European Neogene. It is rarely absent from Pliocene and Miocene pollen assemblages throughout Europe though it attains a slightly higher quantitative occurrence in the Pliocene (Altehenger, 1959; von der Brelie, 1959 and 1967) and for this reason is included by both these authors in the Pliocene element (see Section VI).

Thomson and Pflug (1953) compared five of their form taxa to the genus, but each type has a similar stratigraphic range, so that the subdivisions have little value at the present. Zagwijn has mentioned a form with a relatively thin exine and with more or less equatorial pores, which he says is generally restricted to the Tiglian: this form is not met with in the Derbyshire material.

The ecological implications of the occurrence of *Carya* have been mentioned by Chaloner (1968) when discussing the presence of the genus in the Paleogene of S.E. England, suggesting that it occupied the wooded hinterland rather than the *Nipa* swamps which are generally associated with the deposition of the London Clay. The genus's common occurrence in Europe during the Tertiary makes an interesting comparison to the present distribution pattern, some species being restricted to North America whilst the others are limited to S.E. Asia. It is unlikely that palynology will ever be able to provide accurate specific identifications of the fossil material in terms of the extant species, with the object of relating the European occurrence with those of either the Old or New Worlds.

ULMACEAE

52. *Ulmus* sp.

(Pl. 8, Fig. 8)

The genus is commonly recorded throughout the European Tertiary and Pleistocene. In most Neogene records, including this one, the pollen is present very infrequently. The pollen grains are about $25\ \mu$ in diameter, coarsely rugulate, with up to ten irregularly spaced pores.

AQUIFOLIACEAE

53. *Tricolporopollenites iliacus* (R. Pot.) Th. & Pf.

54. *T. margaritatus* (R. Pot.) Th. & Pf.

(Pl. 9, Figs. 1-2)

Both these types have been regularly determined from the European Tertiary and though they have no particular significance to the stratigrapher, their botanical affinity to the modern genus *Ilex* is certainly enough to enable climatic conclusions to be made. Fossil leaf material of the modern genus has been determined from the German Pliocene by Mädlar (1939).

Tricolporopollenites iliacus has very prominent clavate sculpturing which tends to conceal the pores and colpi. Thomson & Pflug (1953) separated the form species into two form subspecies on the basis of their size, f. *major* having a longitudinal dimension greater than $45\ \mu$ whilst f. *minor* is from $25\text{--}45\ \mu$. Both forms have been identified from the Derbyshire assemblage. Pons (1964) suggests affinity of this form species to *Ilex aquifolium*, pollen of which has been commonly described from Pleistocene deposits; the same modern species was determined by Mäddler for his macrofossil material. Three fossil species of the genus are mentioned by Gothan and Weyland (1964) in reviewing the macrofossil record, though only one of these is from the Neogene.

Tricolporopollenites margaritatus has much smaller clavate structures than the previously mentioned type, and is about $30\ \mu$ in length. Pons (1964) compares this form taxon with the Recent *Ilex canariensis*. But this and other attempts to relate either the fossil pollen or leaves of this plant to modern species is tentative, despite the unusually distinctive characters of the material. Both *Ilex* and another genus represented in the Derbyshire assemblage, namely *Hedera*, are useful climatic indicators. Experiments on both these genera (Iversen, 1944) show that the modern European species are intolerant of a mean monthly temperature which falls below -0.5°C . The implications of this are reflected in the distribution map of the species (Godwin, 1956), where the plants are shown to be absent from northern and continental Europe—regions of low oceanicity. In the fossil record however, there are Tertiary records of the genus from parts of Europe that are continental in climate (Pactova, 1966; Mazancova, 1962—both in Slovakia; Doktorowitz-Hrebicka, 1964—Poland). A similar state of affairs has been explained for *Tsuga*, though in that case, the possibility that the European occurrences are of an extinct species favouring more diverse climates is another possible explanation. Alternatively, Central Europe may have had less severely cold winters than now, or else the fossil species of these genera were able to withstand lower temperatures than the extant ones.

SAPOTACEAE

55. *Tetracolporopollenites sapotoides* Th. & Pf.

(Pl. 9, Fig. 3)

Thomson & Pflug (1953) made tentative comparison of seventeen taxa to this family; this diversity, together with the form's similarity to the tricolporate *Nyssa*-type (Doktorowitz-Hrebicka, 1964 identified very similar tetracolporate pollen as *Nyssa*) make any comparison to modern genera rather dubious.

The occurrence of pollen from this family is mainly restricted to the European Miocene (v.d. Brelie, 1967; Potonié, 1967) though Pons (1964) has made one of the few determinations from Pliocene strata. This Derbyshire record represents the youngest record of the family in the more northerly latitudes of Europe.

ERICACEAE

- 56. *Empetrum* sp.
- 57. *Calluna* sp.
- 58. *Erica* sp. ?
- 59. *Rhododendron* sp. ?

(Pl. 9, Figs. 7-11)

Although the recognition of pollen from this family is a simple matter—in most of the genera the pollen grains are united as tetrads—distinction at the generic level has never been fully investigated. One of the fullest accounts of the pollen morphology of extant members of the family has been given by Oldfield (1959), whilst for Tertiary material, most authors do not even attempt to refer specimens to living genera. In these cases, use is most often made of the form taxa *Tetradopollenites callidus* (R. Pot.) Th. & Pf. and *T. ericius* (R. Pot.) Th. & Pf., which have been described throughout the European Tertiary.

In the Derbyshire assemblage, pollen of the Ericaceae forms a very high percentage of the total pollen count (Fig. 6) and examination of the material reveals at least four morphological types. Comparison of these forms to modern reference material was found to be of little value due to the great variation in pollen morphology within each very large genus. The identifications that have been made here are based on the conclusions of Oldfield's work.

Pollen tetrads assigned to *Empetrum* sp. are of compacted shape, often rounded or sub-triangular, with thick inner walls. The exine has a finely verrucate ornamentation, whilst in most specimens in the Derbyshire material both the pore and furrow were indistinct.

Calluna sp. tetrads have been identified by their loose and irregular shape. The exine, which is thinner than in the other tetrad genera of this family mentioned here, has an irregular verrucate ornamentation.

Both *Erica* and *Rhododendron* have a very large number of modern species and distinction of their pollen tetrads is difficult even at the generic level. The recognition of the two separate genera in this assemblage must be regarded as tentative. Chief among the apparent differences in pollen morphology of the two genera is the nature of the exine. In *Erica*, ornamentation is very faint, whilst the walls of *Rhododendron* tetrads are prominently reticulate.

ONAGRACEAE

- 60. *Corsiniipollenites maii* Kr.

(Pl. 9, Fig. 5)

The easily recognized triporate pollen from plants of this family usually occur in Tertiary deposits in very small quantities. Though present throughout the whole Tertiary in Europe, most form taxa have been described from the Pliocene (Krutzsch, 1968).

Although some modern species in the family are trees and shrubs, the great majority, including those living in and around Europe, are of herbaceous habit. If,

as seems likely in this case that the pollen is from a herbaceous plant, then it represents one of the few instances of plants of this habit (among the dicotyledons) that have been identified from the Derbyshire assemblage. There are without doubt pollen grains from many other herbaceous genera that have been examined and passed unidentified in the Derbyshire material ; but they are of very rare occurrence, and are dissimilar from any previously described material. Rather than formally describe and illustrate these forms, to no currently useful geological or botanical purpose, the forms are not mentioned qualitatively in this work.

COMPOSITAE

61. *Compositoipollenites rizophorus* R. Pot.

(Pl. 9, Fig. 4)

Another rarely occurring herbaceous plant record is of pollen from the Compositae. The pollen is about 20 μ in length, covered with spinules up to 3 μ in length with a swollen base. Enough is known of the detailed palynology of this family (Wodehouse, 1935) to justify no generic assignation being made. Few modern species of the family are trees or shrubs however, suggesting, along with the infrequent occurrence of the pollen in this Derbyshire material (and in other Tertiary assemblages) that the parent plant was of herbaceous habit.

A number of Tertiary pollen assemblages refer to this type as Compositae-type, though Potonié (1960) based the name used here, *Compositoipollenites rizophorus*, on type material from the Eocene of the Geiseltal. This is similar enough to the Derbyshire specimens to allow the use of this name here. *Pollenites echinatus* Pot. & Ven. (1934), similarly assigned to this family by some authors (Potonié et al., 1950) is larger than the Derbyshire specimens, with longer and broader spines.

LILIACEAE

62. *Periporopollenites echinatus* (Wodeh.) Th. & Pf.

(Pl. 9, Fig. 6)

Wodehouse's (1933) original description of *Smilacipites echinatus* suggests a likely similarity of these pollen grains to those from the genus *Smilax* ; an assignation endorsed by Thomson & Pflug (1953). The rare Derbyshire specimens have the same type of spines ; and since leaf material of the genus *Smilax* has been identified from cuticle remains in the same deposits, the assignation is further supported by this study. The Derbyshire material of *P. echinatus* is distinguished from composite pollen by its precisely spherical shape, fewer spines per unit area, the absence of 3 colpi, and the lack of a basal thickening to the spine structures. The only other fossil pollen of possible relation to the genus *Smilax* which has been previously recorded from the European Neogene is that referred to *P. echinatus* by Neuy-Stolz (1958). Macro-fossil material however has been described as *Majanthemophyllum petiolatum* (Web.) Wey., from the German browncoal (Weyland, 1957), whilst leaves

of the modern mediterranean species *Smilax aspera* have been found in the Italian Pleistocene.

GRAMINAE

63. *Graminidites media* Cookson 1947.

(Pl. 9, Figs. 12-13)

These pollen grains are up to 35 μ in diameter, have a single protruding pore, with a minutely tegillate exine. The earliest reliable palynological record of pollen from this family is from the Lower Oligocene of New Zealand (Couper, 1960) though Chandler (1964) has reported possible leaf remains from the Palaeocene of southern England. Throughout the Neogene of Europe, this pollen, as in Derbyshire, occurs in very small numbers, though it is of very wide geographical distribution.

V. QUANTITATIVE ANALYSIS

The Derbyshire Localities

A brief description of the deposits which bear the palynological assemblage has been given in an earlier publication (Boulter & Chaloner, 1970). Plant bearing grey clays, overlying variously coloured clays and sands have been found at Bee's Nest pit Brassington, and again some 7 Kms. to the north west at Kenslow Top pit, Friden. The fossil remains are found only at these two of the sixty or so of the sink-hole deposits; these are all thought to have formed by collapse of the sands and clays into sink holes in the Carboniferous limestone which outcrops in this part of north Derbyshire and east Staffordshire. Ford & King (1968, 1969) have documented geological evidence to explain the mechanism of the deposits' origin. During the Tertiary, the limestone, with well developed solution cavities, was covered with sands and clays. Plant fossil remains survive in the uppermost clay, which is thought to have been deposited towards the end of this period. Intermittent collapse of the cavities is thought to have let down the Tertiary cover to produce the infilled sink hole structures, which are currently being worked for the silica sands. Comparable catastrophic events have been observed recently (Foose, 1967) in South Africa, producing a similarly disorganized infill of sediment in limestone sink holes.

The form of the plant bed at Kenslow Top pit is different in several respects to that at Bee's Nest pit, though the relation of each bed to the underlying clays seems to be comparable. At both localities, the plant bearing clay lies above a paler grey clay, and is situated in the estimated centre of each sink hole. The Bee's Nest deposit is much smaller than that at Friden; on the surface at the present time, about 9 square metres is all that is exposed. Throughout the whole deposit, dark grey pollen bearing clay is mixed with the same kind of pale grey unfossiliferous clay which underlies the plant bed. In no part of this plant bed at Bee's Nest pit has an uncontaminated block of fossiliferous clay larger than about 10 cu. mls. been found; throughout the whole deposit both horizontally and vertically, pieces of plant bearing clay are graded within the pale grey clay matrix, as shown in Figure 2. Consequently it has not been possible to obtain a series of samples which are consistent with conventional

deposition of a continuous nature. Quantitative comparisons have been made of samples from different positions in the deposit, but they show little variation from the single set of results given below in Figure 5. Towards the edge of the Bee's Nest plant bed, the number of fossiliferous pieces of clay suddenly diminishes without apparent bedding changes, to be completely replaced by the pale grey clay matrix (Fig. 2).

The plant bed at Kenslow Top pit is exposed for some 25 metres at the working

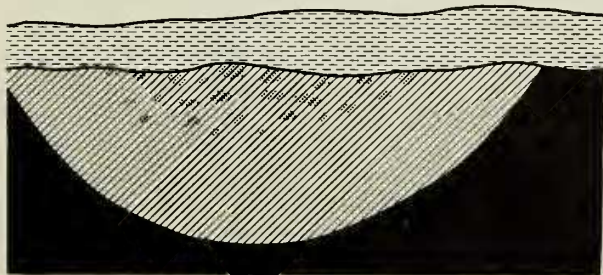


FIG. 2. Postulated section across the plant bed at Bee's Nest pit, Brassington. The plant bearing clay (stippled) is in the form of small blocks up to 100 mms. across, mixed into pale grey unfossiliferous clay (diagonal lines). The bedding of the underlying sands and clays (solid black) is folded to form a geosynclorium. Before excavations began, the bed was covered with 2-3 metres of glacial till (dotted lines). The figure is not drawn to scale; at present, about 9 sq. m. of plant bed is exposed.

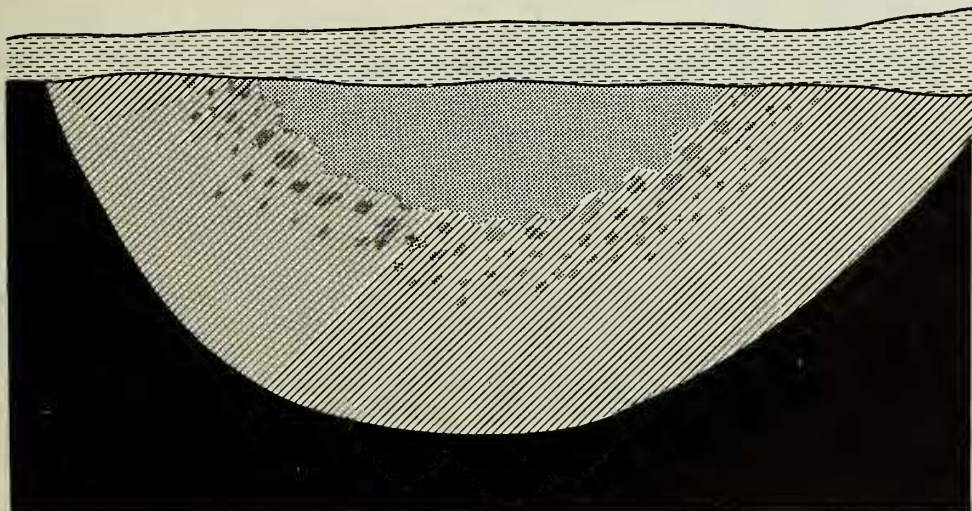


FIG. 3. Postulated section across the plant bed at Kenslow Top pit, Friden. The plant bearing clay (stippled) is in the form of a plano-convex lens, about 6 m. wide and 3 m. thick at the centre. At the lower edge of this block small pieces of plant bearing clay are mixed in with pale grey unfossiliferous clay (diagonal lines). The bed is covered with 2-3 metres of glacial till (dotted lines).

face of the pit, though debris and overwash cover the exposure at one end so concealing the true horizontal extent of the once exposed face. Information that has been obtained from quantitative palynological analysis of samples from both the horizontal extent of the exposed face and from a vertical section of the deposit make

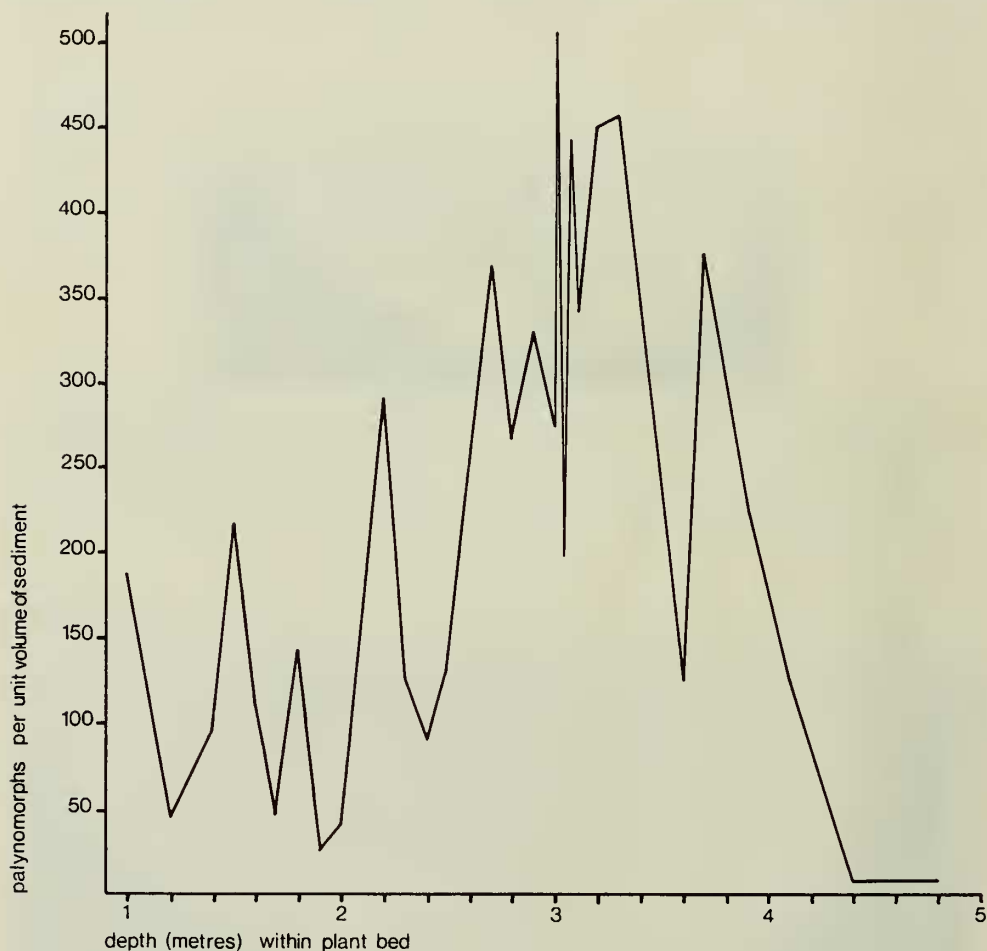


FIG. 4. The change in Absolute Pollen Frequency with depth at Kenslow Top pit. Count of the total number of pollen and spores were obtained from macerations of samples taken every 80 mm. through most of the section, though at the 3 metre depth, samples from every 10 mm. were used. Details are given in Section III of the way in which a standard volume of clay was macerated to produce preparations of comparable pollen and spore concentration.

this site more informative than that at Bee's Nest pit. The larger plant bed at Kenslow Top pit suggests that more of the plant bearing clay was let down into this sink hole during the process of collapse. The plant bearing bed here is not only thicker but the upper part has a smaller proportion of pale grey clay, whilst the lower

part is made up of irregular patches of pale and dark grey clay. The apparently plano-convex lens-shaped block has a much higher concentration of palynomorphs than that of the surrounding mixed material (Fig. 3). It is about 6 metres in horizontal extent (along the exposed face) and a borehole which has been sunk in the central part shows its thickness to be about 4 metres. Analysis of the pollen and spores from this borehole shows sudden changes in their concentration within the sediment (Fig. 4), whilst the relative proportion of different species remains remarkably constant. Examination of the deposit itself reveals no regular bedding planes *in situ*. The plant bearing clay which surrounds this lens shaped portion both laterally and below is itself mixed with the paler unfossiliferous clay in much the same way as that at the Bee's Nest locality. This mixed material is up to 4 metres in thickness, and maintains a much reduced concentration of palynomorphs (Fig. 4, $4\frac{1}{2}$ m. depth). The concentration is low even in the small patches of purely plant bearing clay, whilst the pale grey clay mixed with it is completely unfossiliferous. The low concentration then is not necessarily due only to the effect of mixing, but also to a slight facies change which itself caused a change in clay colour from pale grey to the darker browner grey colour of the plant bearing material.

Kenslow Top pit, Friden.

Macerations have been made by the methods described in Section III from samples collected from the surface of the exposure, and from the borehole mentioned above. This has led not only to a quantitative analysis of the assemblage both horizontally and through the section itself, but also to a comparison of the concentration of the palynomorphs in each clay sample. The graph (Fig. 4) plotting the number of pollen grains per unit area against depth shows seven peaks when samples are macerated from every 80 mms. To check the consistency of this variation, samples from each 10 mms. along a small part of the borehole section were macerated (Fig. 4, 3 m. depth). The results show that there are many more peaks than are shown from the more widely separated samples. Nevertheless, it is thought that sufficient results have been obtained to show that the palynomorph concentration is very variable in vertical section.

Bee's Nest pit, Brassington.

Since the plant bearing clay at this deposit is of smaller proportions and more completely mixed with unfossiliferous clay, no samples have been obtained from a productive sequence. Those that have been examined come from parts of the flat exposed surface of the deposit and also up to 1 metre below the surface, and are, in each case, mixed with the unfossiliferous pale grey clay. The concentration of palynomorphs in these samples is variable but in no apparently meaningful way, due to the complex mixing that has occurred. Quantitative analysis of the major taxa from the samples examined produces results similar to those shown in the histogram for sample V.55635 (B.M. number) (Fig. 5).

Interpretation of the absolute pollen frequency (A.P.F.)

The results of A.P.F. counts from samples in the vertical section at Kenslow Top

pit have been mentioned above, and are recorded in Figure 4. There is insufficient evidence available to make any indubitable interpretation of the variation in the palynomorph concentration, though several suggestions can be briefly mentioned.

The method of origin of the sink hole deposits may have been responsible for the variation, in which case the geomorphological events that led to the formation of the sink hole deposits would be of significance in any interpretation. These events themselves however, are controversial (Boulter & Chaloner, 1970) though it seems most likely that collapse occurred during the Tertiary (Ford & King, 1969) rather

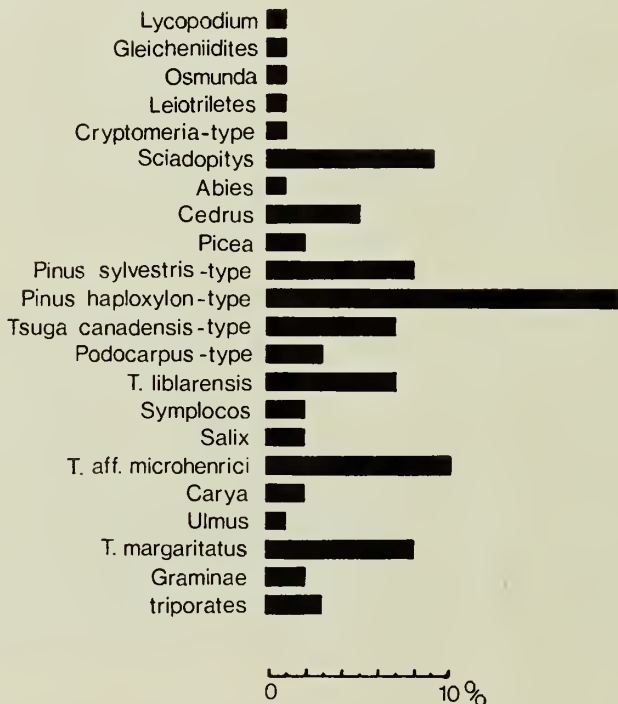


FIG. 5. Histogram showing the percentage occurrence of pollen and spores in clay sample V 55635 from Bee's Nest pit, Brassington. There was no significant variation from these results in other samples from that deposit that have been analysed.

than earlier (Kent, 1957). There is no firm evidence to confirm that the plant bearing clay either slumped into the sink holes together with the other unfossiliferous sands and clays, or whether the plant bed was deposited above the pale grey unfossiliferous clay soon after collapse had occurred. Quantitative results show that despite the change in Absolute Pollen Frequency, the concurrent composition of the assemblage is constant. In view of this constancy, had the plant bed collapsed into the sink hole at the same time as the underlying clays and sands, the sediment may have become distorted by mixing and cracking, with subsequent weathering producing the present fluctuating concentration of palynomorphs. On the other hand,

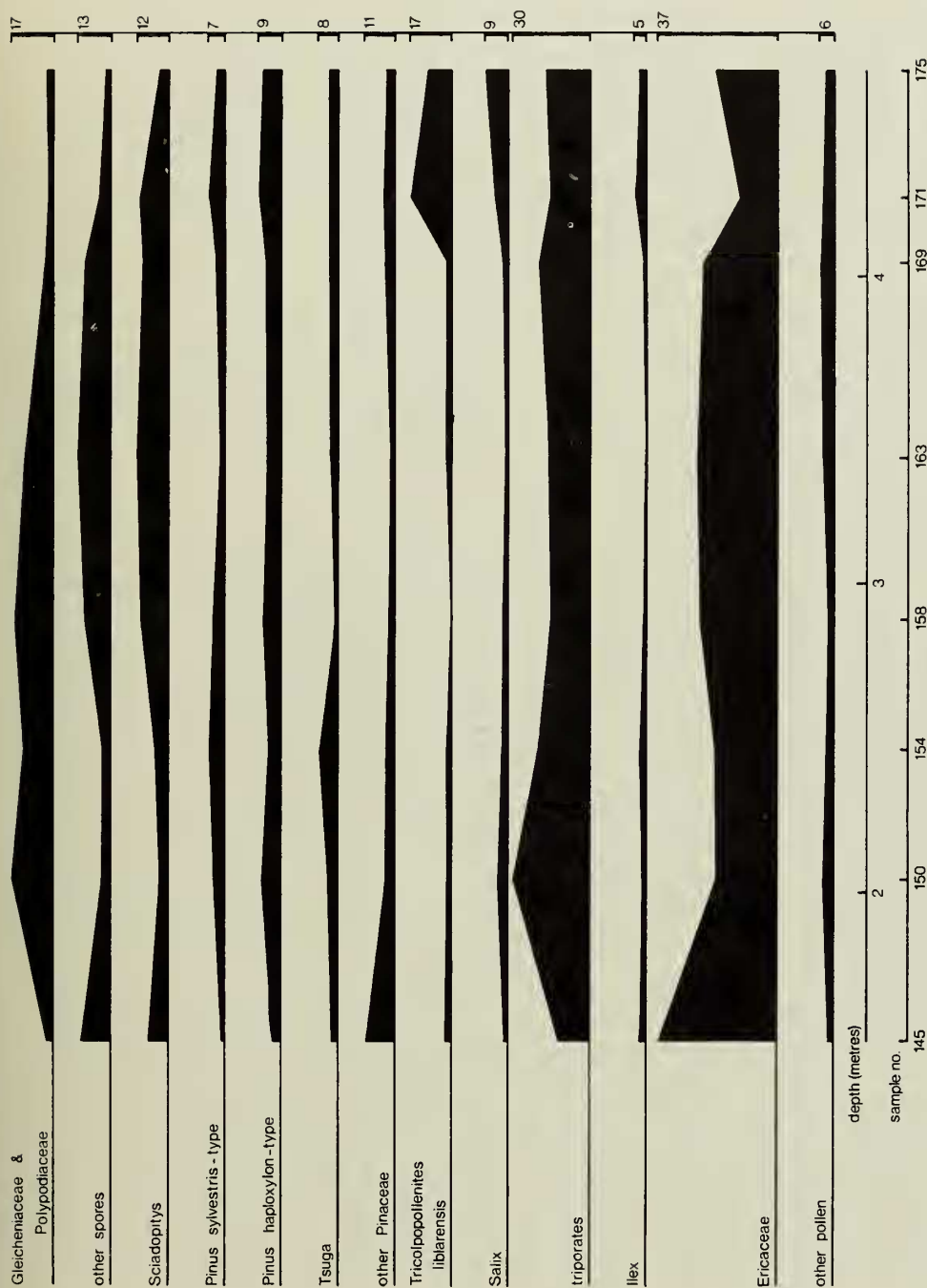


FIG. 6. Pollen diagram through the section at Kenslow Top pit, Friden. Values showing the depth within the section were measured from the base of the glacial till, and the column to the right of the diagram shows the maximum percentage occurrence of each type.

had the plant bed been deposited after collapse, reworking from the immediate vicinity of the infilled sink hole, with (seasonal ?) variations in the rate of deposition, could have produced the changes in the A.P.F. that have been recorded.

Other interpretations of the change in A.P.F. can be made on the assumption that the geomorphological events that may have occurred did not have a direct influence on the distribution of the plants in the deposit. Climatic variation and forest fire are thought to have been common events in Europe during the Neogene (Ahrens & Lotsch, 1967 ; Teichmüller & Teichmüller, 1968) and are characterized by changes in both the rate of pollen production and the type of vegetation cover. However, results from quantitative analysis of individual members of the assemblage show little change throughout the section (Fig. 6), so that such explanations are most unlikely. Details of the changes in A.P.F. show that at the 3 metre part of the section, the palynomorph concentration was at a maximum. The proportion of the warmth-loving Tertiary Component (see Section VI) increases here too, suggesting that there may have been a climatic fluctuation at the time represented by this part of the section, even if the absolute change were explained by a decrease in the rate of deposition with a consequent increase in the A.P.F.

Comparative interpretation of the quantitative analysis

For purposes of this analysis, it has been necessary to compromise on the recognition of many of the pollen and spore types. At many horizons it is not always possible to assign all specimens to one of the taxa reported above. This is due to the frequently obscure specimens in the maceration samples, which are often badly preserved, broken, or hidden by detritus. For example, distinction between *Myrica*, *Corylus* and some specimens of *Betula* necessitates perfect preservation of the exine at the pore regions ; the pores must not be obscured in any way. This ideal situation is rare in practice, so that although the distinctive features of each type are occasionally available (from which specimens the qualitative descriptions in Section IV have been made), all three types are grouped together for quantitative purposes. It has been possible to designate these groups so as to keep separate not only the members of the Tertiary Component, but also what can be regarded as the most plausible major ecological associations. So it is hoped that despite the hazards of grouping different taxa together, significant conclusions can still be made from the quantitative results.

Although the two Derbyshire deposits are separated from one another by only 7 Kms., a comparison of the quantitative results shows important differences in their floristic character. The Kenslow Top assemblage represents two distinct associations : heath and woodland. The heathland element contains plants from the Ericaceae, *Myrica*, *Salix*, *Sphagnum*, *Lycopodium* and some conifers, whilst the woodland is made up of the conifers, deciduous trees and ferns, such as *Lygodium*, *Polypodium*, *Gleichenia* and *Pteridium*. The ecological implications of these associations will be discussed in Section VII. Pollen analysis from the Bee's Nest pit however, shows an absence of pollen from the Ericaceae, and lower values of both spores and triporate pollen. The increased values for pollen from the woodland association suggest that this is the only environment which became preserved here.

During the time represented by the 3 m. maximum A.P.F. in the Kenslow Top section, the woodland association forms a larger part of the total pollen count. Most of the members of the Tertiary Component are represented in the woodland association, so it is likely that during this period of deposition the environment was more densely wooded, perhaps as a result of a milder climatic phase. This situation is more prominent at the Bee's Nest pit, where the whole assemblage represents the woodland association. Consequently the Tertiary Component here forms a higher percentage (67%) of the whole assemblage, due to the fact that this deposit is 7 Kms. to the south of Kenslow Top pit, and thus was further from the Neogene heath.

VI. AGE DETERMINATION

The fossil record from Neogene times shows that there are noticeable differences in the character of these assemblages and those from other provinces at similar latitudes, for example in different regions of Russia (Pokrovskaya, 1956) and Western North America (Wolfe, 1969). This is thought to be due to migration of the temperate flora from the Arctic south to most land masses in the present temperate regions. But due to the different events that occurred during migration, the temperate element in the N.W. European Neogene is different to that in other provinces (Leopold, 1970). There is sufficient similarity however, between the Derbyshire assemblage and those from deposits of similar age on the continent of N.W. Europe, to assume that all are part of the same floral province with a common origin.

Analysis of the major palynological assemblages that have been described from the Neogene of N.W. Europe shows that some taxa only survived in this region during that time. These forms, known as the European Neogene Component, were plants deduced to have migrated south as one province of the Arcto-Tertiary flora, and others that have remained in N.W. Europe throughout the Tertiary. Among both groups there were newly evolved taxa which are not present in Palaeogene floras either in N.W. Europe or in Arctic regions. It is the proportions of each taxa in any one assemblage that can give us clues to the age of that assemblage, if factors such as environment and location are taken into account. Comparison of palynological assemblages in the N.W. European province have enabled Zagwijn (1960), von der Brelie (1959) and others to designate various taxa to this Neogene Component. They were also able to divide this component into a Miocene Element and a Pliocene Element, as shown in Table 2. Von der Brelie has recently (1967) summarized the fossil record of some of the palynomorphs throughout the German Neogene, though slight variation in this can be expected for the European province as a whole, if only from the varying influence of the Alps and the Atlantic Ocean within this region.

Our understanding of the role of this Neogene Component seems to offer a reliable method for determining the age of European Miocene and Pliocene pollen assemblages. The present author has plotted the total number of elements within the Miocene and Pliocene Components (as listed in Table 2) from some of the better known European assemblages, against their approximate age. This curve is shown in Figure 7. The age determinations used in the curve are those of the investigator of the particular flora; though in the case of floras of closely similar age, an accurate sequence along the x axis is not possible due to vertical deviation from the curves of up to about 10%.

This method leads to the conclusion that the Derbyshire assemblage is of a Miocene/Pliocene boundary age : an age rarely if ever, represented by non-marine deposits in N.W. Europe.

TABLE 2

Pollen taxa which have been cited (von der Brelie, 1959 ; Zagwijn, 1960) as members of the Pliocene and Miocene Components. Those marked with an asterisk are present in the Derbyshire assemblage.

PLIOCENE ELEMENTS	MIOCENE ELEMENTS
* <i>Pinus</i> haploxydon-type	<i>Engelhardtia</i> sp.
* <i>Sciadopitys</i> sp.	<i>Tricolpopollenites henrici</i>
* Taxodiaceae	* <i>T. microhenrici</i>
* <i>Tsuga</i> spp.	* <i>T. liblarensis</i>
* <i>Nyssa</i> sp.	<i>Cupuliferoipollenites villensis</i>
* <i>Liquidambar</i> sp.	<i>Tricolporopollenites pseudocingulum</i>
* <i>Carya</i> sp.	<i>T. cingulum</i>
<i>Pterocarya</i> sp.	<i>T. megaexactus brühlensis</i>
<i>Castanea</i> sp.	<i>T. euphorii</i>
<i>Tricolpopollenites parmularius</i>	<i>T. microreticulatus</i>
	* <i>T. edmundi</i>
	* <i>Symplocos</i> spp.

The individual taxa making up both the Miocene and Pliocene Components which are listed in Table 2 have their origins from two major sources. Either they are the products of the southerly migration from the Arcto-Tertiary flora, or else they have evolved from elements which occurred in N.W. Europe during the Palaeogene. A comparison of the living plant genera or those modern genera thought to have affinity with the pollen form species, listed in Table 2, with those present in the Palaeogene of southern England (Chandler, 1964) and the Arcto-Tertiary flora (Chaney, 1947 ; Takhtajan, 1969 ; Manum, 1962) shows that all genera were present within all three geofloras. This means that despite the presumed migrations up to and down from the Arctic, all the genera concerned remained distinct and changed in form only slightly (which we record as change in species). Within the limits of palynological identification to the modern generic level, it is possible to conclude that no major genus in the Neogene of N.W. Europe occurred in the Palaeogene Arcto-Tertiary flora without having representation at that same time in the warmer climates immediately to the south. This accords well with the views of Stebbins (1950, p. 526) that "since the beginning or end of the Eocene . . . in temperate regions few, if any, new genera have appeared".

Since the Eocene then, plants in temperate climates are thought to have evolved only at the specific level, so that generic changes in the floras of these regions have been mainly due to migration. Both the Miocene and Pliocene Components in the Derbyshire assemblage represent separate definable waves of this migration process, which was brought about by the cooling climate. As this cooling became established, plants of the Miocene Component were the first to become extinct in this region

(Leopold (1968) used the term "extirpation" for this phenomenon), and were replaced by plants of the Pliocene Component which were presumably able to withstand slightly lower mean temperatures. These movements south have been recorded in southern France (Pons, 1964) where pollen of the N.W. European Miocene component is found in fairly large percentage frequency in deposits of roughly middle Pliocene age.

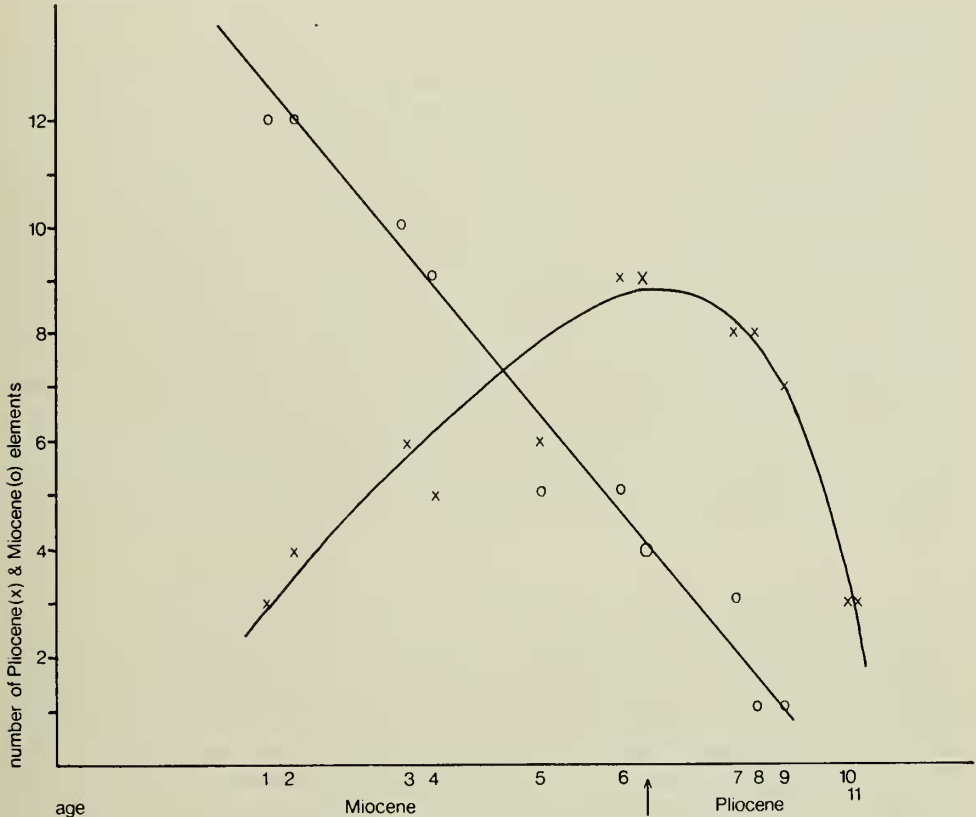


FIG. 7. Change in the number of Miocene (o) and Pliocene (x) Elements (see Table 2) present in eleven Neogene assemblages that have been described in the papers listed below. The numbers along the x axis refer to these eleven assemblages, though the sequence in which they are arranged along the axis is of little correlative significance, since the axis does not follow any accurate scale.

The arrow shows the age of the Derbyshire assemblage as determined by this method.
 1. Upper Miocene. Neuy-Stolz, 1958. 2. Upper Miocene. Kremp, 1950. Steinberg no. 12. 3. Upper Miocene. Kremp, 1950. Delliehausen no. 6. 4. Upper Miocene. Pacltova, 1966. 5. Upper Miocene. Mazancova, 1962. 6. Branssumian. Zagwijn, 1967. Born 1 and 2. 7. Susterian. Zagwijn, 1960. Koningsbosch, Plate 9. 8. Upper Pliocene. Leschik, 1951. Flöz 1. 9. Reuverian. Altehenger, 1959. Wallensen (K). 10. Reuverian. Zagwijn, 1960. Susterian Diagram, Plate 11. 11. Tiglian. Zagwijn, 1963. Tegelen Diagram.

The precise destiny of this Neogene Component after the end of the Pliocene is not clear. Many of its elements, such as *Carya*, *Tsuga*, and the Taxodiaceae are now only native to very restricted regions of N. America and E. Asia : regions upon which the N.W. European Component can have had no direct influence. This suggests that by the end of the Early Pleistocene many species of the Component became extinct in N.W. Europe ; perhaps their routes of migration were blocked by the Alps and the Mediterranean (Takhtajan, 1969, p. 204) but there is no direct fossil evidence for this.

The possible complete extinction of most members of the N.W. European Neogene Component reinforces the argument that has been used several times in the systematic part of this paper that its species are dissimilar from any living today. The two species of *Tsuga* represented in the pollen of the Derbyshire assemblage (and which occur abundantly in Neogene deposits throughout Europe) are unlikely to have had any contact with the living *Tsuga canadensis* or *T. diversifolia* since the time of the Arcto-Tertiary flora. Since then, the Atlantic Ocean isolated the North American species from other members of the genus in S.E. Asia and Neogene Europe. Had *T. diversifolia* stretched right across Eurasia during the Neogene, surely the species would now occur in the Near East (as for instance does *Cedrus libani* ; this genus is represented in the Derbyshire Neogene) or say in the southern part of Asia. The occurrence in N.W. Europe during the Neogene, of genera that are now isolated by both the Atlantic and Europe are more likely to have migrated from a point of common origin in the north than to have had originally a continuous wide distribution. The European Neogene would have been a third area that the same genera colonized during this time, very likely as distinct species that are now extinct.

VII. THE NEOGENE ENVIRONMENT IN DERBYSHIRE

The distribution of the fossil plants as well as the nature of the clay itself, has led to the conclusion that the material of the plant bed has been deposited subaqueously. The underlying sands and clays also show evidence that they have been deposited under similar conditions, perhaps as a result of more rapid flow, since signs of current bedding are preserved in parts of the sand deposit at Kenslow Top pit. The present limestone surface in which the sink hole deposits occur forms what Linton (1956) has called the Peak District Upland Surface, and this, during late Tertiary times (as now) lay to the south of the much higher Holme Moss Surface (Sissons, 1954) of Millstone Grit. So it seems acceptable to suppose that the Holme Moss Surface of Neogene times provided the source of fluvial activity which gave rise to some of the sands and clays which are found today in the sink hole deposits. The only direct evidence for this within the sink hole deposits themselves (apart from the current bedding features) can be found at the most basal part of the Kenslow Top pit plant bed. In the clay at this part of the bed (which is below the section shown in Figure 6), re-worked Namurian miospores (Neves, 1958) form a significant part of the assemblage ; they do not occur at all however in the major part of the plant bed, nor in any other of the deposit's sands and clays. Indeed, the sands and pebbles of the pocket

deposits are thought to be dominantly derived from the retreating Triassic scarp to the south (Ford & King, 1968).

Current geomorphological theory suggests that during Oligo-Miocene times, Pennine uplift caused the Derbyshire limestone to assume a significant height above sea level (Linton, 1956). It may have been as a result of these movements that a river system from the higher Holme Moss Surface became well established, and that deposition of the plant bed subsequently occurred.

Analysis of the fossil plants present in the Derbyshire assemblage does not help very much in determining the exact nature of the fluvial process that is thought to have been concerned with deposition. The only aquatic (or swampy) forms present in the pollen assemblage (in very small quantities) are *Taxodium*-type and *Nyssa* sp., both of which are difficult to assign either to modern species of known ecological character, or to other fossil types which have been described from deposits of freshwater origin (e.g. Szafer, 1954). This scarcity suggests that the pollen-bearing clay was deposited by either a slowly moving river or else by the reworking of Neogene sediment of unknown form which might have occurred around the collapsed sink hole (see Section V, page 396). The two plant associations that have been identified from the quantitative analysis of samples from Kenslow Top pit can be interpreted as occupying separate parts of the Neogene surface in Derbyshire; the Ericaceous heathland for instance on the higher and more northerly (and therefore more distant point from Bee's Nest pit, where the association is poorly represented) Holme Moss Surface, whilst the woodland association occupied the intermediate neighbourhood near the deposits themselves. But the structure of the Neogene vegetation could have been more complex than this, as will be appreciated by comparison to the modern vegetation patterns of the region today. The Neogene environment is likely to have been simpler than the modern one, due to the absence then of glacial till and the existence of a younger landscape, but local niches could have existed for example possibly on exposed dolomite tors (it is debatable if these were exposed during the Neogene) or in river valleys. Although such niches are of common occurrence in temperate zones, they are absent in most tropical regions (Van Steenis, 1969) and so may have been less common than now in Neogene Derbyshire. Further ecological analysis or comparison of the members of the Derbyshire assemblage with modern plant associations is severely limited by the uncertain specific affinities of most of the important fossil types. There is similar difficulty involved with the deduction (or rather, induction) of climatic influences from the modern genera that we believe to have been present in the Derbyshire Neogene environment. For instance, genera such as *Hedera* and *Ilex* that are regarded as characteristic inhabitants of oceanic climates in Europe today, may have existed during the Neogene as species with different climatic demands. But since different genera even of the same ecological affinity are thought to have evolved at quite different rates (Stebbins, 1950, p. 551 et seq.), climatic trends can be most accurately estimated by considering groups of plants rather than individual genera. It has become general practice for ecologists to separate elements of the modern British flora into various climatically distinct geographical elements (Matthews, 1937), based on their current areas of distribution, not their centre of origin. A similar system has recently been devised for Tertiary

floras by Krutzsch & Majewsky (1967), who separated widely distributed European Neogene palynomorphs into four groups : warm, intermediate, temperate and facies elements. Most members of the first two of these divisions are now extinct in Europe, whilst members of the Tertiary Component (see Section V) are represented in all four groups. The assignments are based on the present climatic requirements of the modern genera with presumed affinity to the fossil forms, and so in some cases may not be correct. On the basis of this work, the Derbyshire assemblage has been separated into climatic divisions which are shown in Table 3.

TABLE 3

Climatic groups of some members of the Derbyshire assemblage, after Krutzsch & Majewsky (1967).

WARM ELEMENT	INTERMEDIATE ELEMENT	TEMPERATE ELEMENT	FACIES ELEMENT
<i>Verrucatosporites</i>	<i>Keteleeria</i>	<i>Tsuga</i>	<i>Pinus</i>
<i>favus</i>	<i>Abies</i>	<i>Neogenisporis</i>	<i>Nyssa</i>
<i>Leiotriletes</i>	<i>Cedrus</i>	Polypodiaceae	<i>Alnus</i>
<i>Podocarpus</i> ?	quercoide types	<i>Picea</i>	<i>Ilex</i>
Sapotaceae	<i>Juglans</i>	<i>Sciadopitys</i>	Taxodiaceae
<i>T. edmundi</i>	<i>Carya</i>	<i>Ulmus</i>	Ericaceae
<i>Hedera</i> sp.		<i>Liquidambar</i>	Sphagnaceae
Symplocaceae		<i>Corsiniipollenites</i>	
		<i>Carpinus</i>	
		<i>Corylus</i>	
		Compositae	
		Graminae	

The modern British flora is distinguished from that of the European continent by the effects of a temperate oceanic climate. West (1961) has suggested that high oceanicity was prevalent during the Early Pleistocene too, encouraging the development of *Empetrum* heathland which had many of the temperate genera that are found in the Derbyshire heathland association. West's comparison of the British Early Pleistocene flora to those of the Netherlands and southern Poland led him to the conclusion that the gradient of oceanicity/continentality of climate across Europe was probably more marked than that at present. At the beginning of the Pliocene however, western and central European floras showed no significant difference either of a qualitative or quantitative type ; genera such as *Tsuga*, *Empetrum*, *Rhododendron*, *Hedera* and *Ilex* which have modern species characteristic of oceanic climate are widely distributed into Central Europe during the Neogene (see for example, Pacltova's (1966) description of the Kovacova flora from southern Slovakia). There are two possible explanations to account for this apparently wide distribution: either the oceanic species cannot be recognized palynologically, or else the warm climate in Europe during the Neogene did not produce the same kind of gradient across the continent that exists today.

VIII. ACKNOWLEDGMENTS

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